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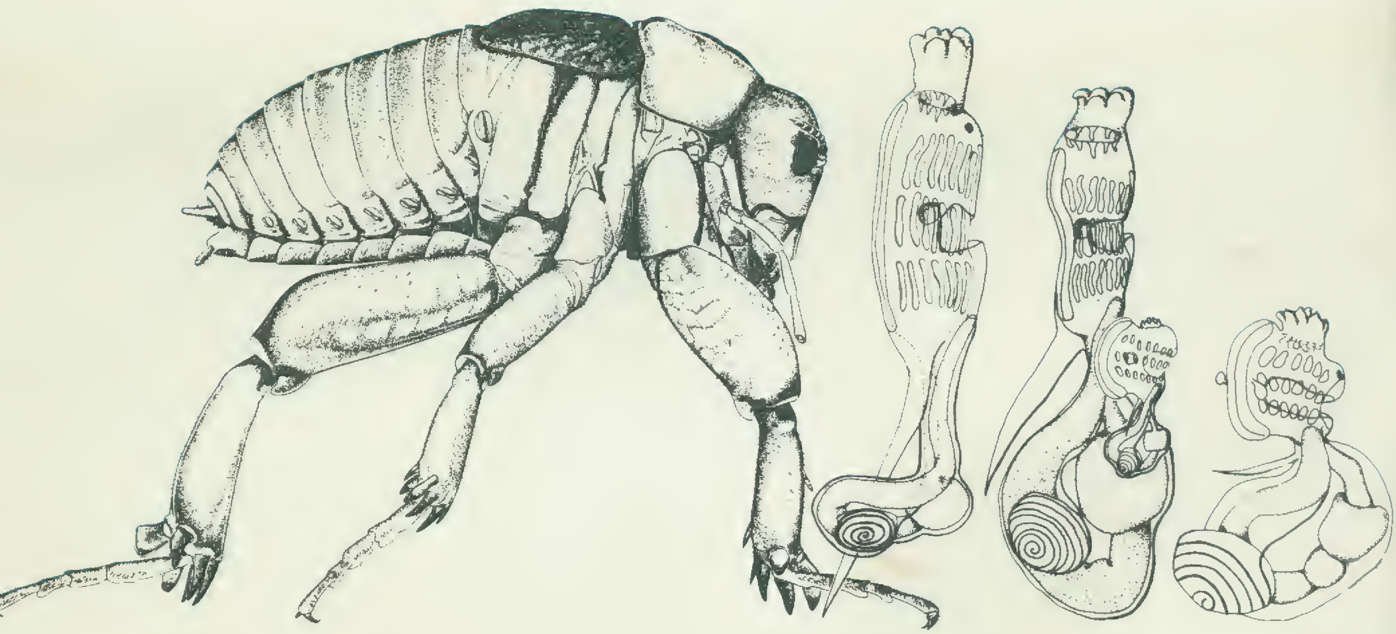

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ALGAL-BEARING DIDEMNID ASCIDIANS IN THE INDO-WEST-PACIFIC

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ABSTRACT

New material from the fringing reefs of Viti Levu and from the Great Barrier Reef form the basis for a review of the taxonomy, phylogeny, habitat, distribution and larvae of 18 species of the family Didemnidae displaying symbiosis with prokaryotic algae. The species are in the genera *Didemnum, Trididemnum, Lissoclinum Echinoclinum* and *Diplosoma,* and include two new species, one of which is endemic and probably isolated in an unusual habitat on the southwestern fringing reefs of Viti Levu.

A remarkable organ for the transference of algal cells from generation to generation in *Diplosoma* spp. is described for the first time. The name *rastrum,* or plant rake, is proposed for this organ.

The mechanism for gene flow in species with a wide range between 30°N and 30°S latitude, and 30°W and 150°E longitude is discussed.

Nine algal-bearing Ascidiacea of the family Didemnidae from the Great Barrier Reef, were formerly reported by Kott (1977). The present paper discusses these and a further 9 species, and represents a review of all the known Pacific Ocean ascidian species that display an intimate association with blue-green algae. A large quantity of material from a wide range of locations (including the larvae and the types of most of the species) has been examined. It has been possible to resolve much of the confusion relating to the identity and synonymy of this interesting, albeit neglected, group of didemnid ascidians.

The species in which plant cells are known to occur are in 5 genera (viz. *Didemnum, Trididemnum, Lissoclinum, Echinoclinum* and *Diplosoma).* The relationship does not appear to have evolved in the two remaining genera of the family *(Leptoclinides* and *Polysyncraton).*

The view that the relationship between plant cells and host is symbiotic is supported by the presence of peculiar adaptations for the transferance of plant cells to the next generation in the 15 species for which larvae are known. In the genus *Didemnum* the larva is known only for *D. molle* and its mechanism for carriage of plant cells is similar to that in *Lissoclinum* spp. *Trididemnum* spp. have different mechanisms; and in *Diplosoma* spp. a unique and previously undescribed organ, the *rastrum* or plant-rake is present (see *D. virens,* below).

In some cases the similarity between these larval adaptations for carriage of plant cells tends to support the view that there are close phylogenetic relationships between groups of species in each of the genera represented. Studies of the plant cells could provide further evidence in this regard. However, the fact that the ascidian/plant cell relationship appears to have evolved separately, and sometimes more than once, in each genus further supports the view that some mutual advantage is derived from the association. The ascidian colony at least provides a habitat for the algae, but it is not known what adaptive advantage is conferred on the ascidian colony by the algae. It should not be overlooked, however, that while other ascidians (including didemnid species) invariably occupy more cryptic habitats in the rubble zone behind the reef crest or in caves and crevices in deeper waters down the slope, certain of these plant-bearing species are extremely common on the reef flat where they are exposed to great light intensity *(Diplosoma* spp. and *Lissoclinum voeltzkowi).* There is a latitudinal gradient in the occurrence of these reef flat species that may result from increasing diurnal temperature range to the south, but may also be affected by light. Olsen (1979) has shown that colonies of *T. cyanophorum* do not grow in the absence of light.

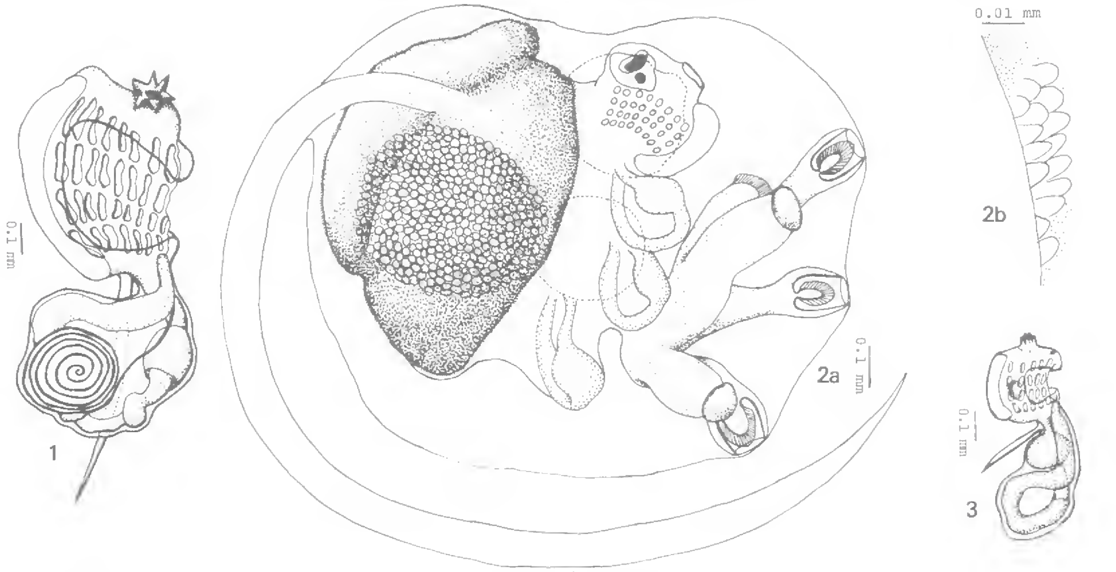
Much of the new material that comprises the basis of this report is from the reef flats of the fringing reefs of Viti Levu. Material from the Great Barrier Reef (Lizard I. and Green I. in the north; Townsville in the central section; and Heron I. in the south) supplements the Fijian collections. Of the wide ranging species in the region, only *Didemnum molle* (> *D. ternatanum:* Kott, 1977) and *Lissoclinum patellum* were not taken from the Fijian reefs. These two species are more often found on the reef slope at a wide range of locations in the Indo-west-Pacific. When deeper waters are sampled, they may be found in the Fijian waters. Only a single new species of *Trididemnum* appears to be endemic in Great Barrier Reef waters. A few endemic species of more restricted range occur but are a relatively rare phenomenon. A new species of *Diplosoma* from Fiji, two new species of *Trididemnum* from the Philippines, and *Diplosoma handi* (Eldredge) from the Caroline Is. are the only plant bearing didemnids that appear to be endemic. It is apparent that there is some strategy available to most species that will ensure gene flow over a wide geographic area.

Although didemnid/algal symbiosis was not thought to occur in the Atlantic Ocean (Kott 1977) it is now known in *Trididemnum cyanophorum* Lafargue and Duclaux, 1979, which occurs in profusion in shallow water coralline habitats off Panama and Guadaloupe. In this large investing species the algal cells are found embedded in the superficial layer of test and not in the common cloaca.

ABBREVIATIONS: The following abbreviations are used below: AM Australian Museum, Sydney; AMNH American Museum of Natural History, New York; AMPI Australian Marine Photographic Index; BM British Museum (Natural History), London; QM Queensland Museum, Brisbane, Australia; USNM United States National Museum, Washington D.C.; ZMA Zoological Museum, Amsterdam; ZMH Zoologischen Staatsinstitut und Zoologischen Museum, Hamburg.

Didemnum molle (Herdman, 1886)
(Figs 1, 2; Plate 1·1)

Diplosomoides molle Herdman, 1886, p. 310. Sluiter, 1909, p. 85; 1913, p. 78.
Not *Lissoclinum molle:* Kott, 1977, p. 618 (< *L. bistratum*). Newcomb and Pugh, 1975, p. 533 (< *L. punctatum*).
Didemnum ternatanum: Van Name, 1918, p. 152. Tokioka, 1955, p. 47; 1967, p. 77; 1975, p. 326. Kott, 1966, p. 287; 1977, p. 618. Vasseur, 1970, p. 213. Newcomb and Pugh, 1975, p. 533. Millar, 1975, p. 229.
Not *Didemnum ternatanum:* Kott, 1972, p. 179.
Didemnum sycon Michaelsen, 1920, p. 44.



FIGS. 1–2: *Didemnum molle* (QM G9780) — 1, zooid; 2, larva (a, from right side; b, ectodermal scales on posterior haemocoelic chamber).
FIG. 3: *Didemnum viride* (BM 07.8.30.41) — zooid.

MATERIAL EXAMINED

NEW RECORDS: Heron I.: January 1976, LWM, QM G9953 (juveniles); March 1975, 18 m, QM G9438 (juveniles); July 1975, 5 m, QM G9439 (juveniles); October 1976, LWM QM G9794 (juveniles); October 1979, LWM QM G12629 (juveniles); December 1976, 9 m, QM G11900 (mature gonads, larvae). Lewellyn Reef: August 1975, 3–9 m, QM G9765 (mature ♂). Lizard I.: June 1976, on coral rock shallow water, LWM, QM G9914 and G9979 (juveniles), QM G9777 (mature gonads some embryos), QM G9778 (larvae); on artificial reef 3–4 m between Lizard I., Palfrey I. and Solomon I., QM G9780 (mature gonads and larvae). Palau Is., 1979, LWM, QM G12680-2.

PREVIOUSLY RECORDED: *Diplosomoides molle* Herdman, 1886, Holotype BM 87.2.4.446. *Didemnum sycon* Michaelson, 1920, Types ZMH K1088, 1089; Van Name det., USNM 7384 (Philippine Expedition). *Didemnum molle > D. ternatanum:* Van Name, 1918, AMNH Chordata 2138, 2139, 2140. *Didemnum ternatanum,* Van Name det., USNM 5982, 2988 (Albatross), 6339; Tokioka, 1967, USNM 11404; Kott, 1977, QM G9652 (juveniles).

DISTRIBUTION

RANGE: Malagasy, Zanzibar (Michaelsen 1920, Vasseur 1970). Western Australia: Cockburn Sound (Kott 1977). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Kott 1977). Indonesia (Sluiter 1909). Aru I. (Herdman 1886). Palau I. (Tokioka 1955, 1967). Philippines (Van Name 1918, Tokioka 1967, Millar 1975). Okinawa (Tokioka 1975).

HABITAT: Specimens have been taken from intertidal to 69 m (Sluiter 1909). Van Name (1918) reported the species growing on coral, shells, eel grass and other ascidians in shallow water. However, most of the stations from which specimens were reported by that author were in waters of 16–40 m, and only a few stations may have been in shallower water. Sluiter (1909) recorded specimens from reefs (intertidal?) to 69 m. In the present collection, the most robust colonies are in fairly protected habitats (in caves, under ledges, and in lagoons) in waters of 2–10 m, usually on dead coral, or rocky substrates. Smaller more or less flat colonies present under boulders near the reef crest, appear only to be juvenile colonies, and seldom achieve the typical hemispherical or stalked facies, although some have been found in pools near the LWM at Lizard I. These soft, flaccid colonies that secrete massive amounts of mucus when disturbed, do not appear to be adapted to intertidal habitats, or habitats on other than firm surfaces.

DESCRIPTION

COLONY: The colonies are characteristically dome- to flask-shaped, with a common cloacal aperture in the centre of the upper surface. Some reach a diameter of 10 cm. They are firmly attached to the substrate by fine strands of spicule-filled test. The surface is smooth with a thin layer of very small spicules (0.005 to 0.015 mm) in the surface test. The spicules, together with a variable amount of brown pigment (especially dense in the vicinity of the common cloacal aperture) affect the colour of the colonies which may be from grey to reddish brown. Spicules are absent from the surface test between zooid openings only in very immature colonies when the green colour of the symbiotic algae is clearly visible. The 6 branchial lobes are conspicuous on the surface, each covered with corresponding lobes of spicule-filled test. One of the most conspicuous characteristics of this species is the soft and easily torn test, and the excessive amounts of mucus that are secreted by the living colonies. The common cloacal cavity is extensive, occupying most of the centre of the colony, and is lined with symbiotic algal cells. Zooids are contained in the soft test strands that cross the cloacal space, connecting the surface to the basal test, or to the core of test that projects from the base up into the centre of the colony.

Juvenile colonies are small, flat and predominantly green, the small spicules being present only around the apertures. In preservative the juveniles are an almost completely transparent reddish brown colour.

ZOOIDS: Zooids are up to 1·5 mm long. The thorax is especially long with 8–10 elongate rectangular stigmata. The wide atrial opening exposes most of the branchial sac. The 6 branchial lobes are pointed and their position where they open onto the surface is clearly marked by the spicules that are contained in the test. There is a long slender retractor muscle. The gut loop posterior to the stomach is curved ventrally. The vas deferens coils 6·5 times around the rather flat ♂ follicle.

LARVAE: These incubate in the central or basal test, the embryo having moved down the test connective in which the zooid is embedded. They are never present in the transparent juvenile colonies, found near the low water mark. The occurrence of these juvenile colonies suggests that breeding occurs throughout the year. Mature

colonies with ripe gonads and sometimes with embryos taken in June, August and December, support this hypothesis.

The larvae are about 0·9 mm long, excluding the tail, which is long and wound three quarters of the way around the larval trunk. There is an oozooid, with ocellus and otolith, and two blastozooids. Anteriorly a more or less rectangular frontal plate, supports the short rather thick stalks of the 3 median adhesive organs. The adhesive cells are arranged in a long rather narrow cone, surrounded by a deep ectodermal cup. As the larva matures, the frontal plate extends forwards on a rather narrow stalk and four long cylindrical ectodermal ampullae are produced from each corner of the frontal plate. There are modified columnar cells on the rounded ends of the ectodermal ampullae. The posterior haemocoelic chamber (erroneously referred to by Kott, 1977, as a 'pouch') into which the tail is inserted, is large and slightly flattened antero-posteriorly. The vacuolated cells referred to by Millar (1975) appear to be yolk cells from the spherical mass of yolk behind the blastozooids. These cells gradually disperse and some are found in the haemocoelic chamber. When the tail is extended the haemocoelic chamber becomes almost spherical and the plant cells adhere to the larval test outside it. A few larvae have been found with the larval tail prematurely withdrawn into this chamber while they are still in the common cloacal cavity of the adult colony (Kott 1977). In the mature larva there are flattened, overlapping scales on the ectoderm of the haemocoelic cavity. Their function is not known, but they resemble ectodermal cells of the rastrum or plant rake in *Diplosoma* spp. and possibly they are associated with the adhesion of the plant cells that cover the test in this region. The two abdominal buds are on the right side of the larva and the thoracic buds are on the left.

REMARKS: The colonies, their spicules, and the copious quantities of mucus that are produced are quite distinctive and the species is readily recognised. The atrial opening that exposes most of the branchial sac, so that the peribranchial cavity is almost entirely lost, is reminiscent of the condition in *Lissoclinum patellum* and *Diplosoma* spp. The larval blastozooids are also reminiscent of the larva of *Lissoclinum bistratum*, as are the modified columnar cells on the ectodermal ampullae. The deep, narrow ectodermal cups and elongate cone of the adhesive organs are unique features of the larva.

Van Name (1918) erroneously identified specimens of this very characteristic species as *D. ternatanum*, and illustrated his description liberally. Subsequent authors accepted Van Name's identification and so perpetuated his mistake. Examination of his specimens, and of the types of *D. molle* and *D. sycon* has established their true identity. Van Name himself was aware of his error, and corrected the labels of these specimens in the American Museum of Natural History.

Colonies have been observed to move up sides of aquaria at 1·5 cm per day over a period of at least 7 days (D. Griffiths, pers. comm.). Movement may be in response to subminimal conditions by successive growth and resorption of adhesive test strands as in *Diplosoma listerianum* (Carlisle 1961). It may cause clustering of colonies observed at the top of *Acropora* debris in lagoons.

Didemnum viride (Herdman, 1906)
(Fig. 3; Plate 1·2)

Leptoclinum viride Herdman, 1906, p. 34.
Didemnum viride Vasseur, 1970, p. 216.
Not *Trididemnum viride:* Tokioka, 1967, p. 87 (< *Trididemnum* spp.).

MATERIAL EXAMINED

NEW RECORDS: None.

PREVIOUSLY RECORDED: *Leptoclinum viride* Herdman, 1906. Holotype, BM 07.8.30.41.

DISTRIBUTION

RANGE: Ceylon (Herdman 1906). Malagasy (Vasseur 1970).

HABITAT: The holotype is from 2·5 m, south of Periya Paar, Ceylon. It is investing a skeletal fragment of *Campanularia juncea* (*fide* Herdman 1906). The specimen from Malagasy is from a blade of sea grass.

DESCRIPTION

COLONY: The colony is an extensive encrusting sheet, about 3 mm thick. The surface is marked into rounded and slightly raised areas by slight depressions over the common cloacal canals. The zooids are arranged along either side of these canals. The branchial apertures are evident on the surface of the colony as minute prominences. In the preserved specimen there is a very thin superficial layer of bladder cells mixed with algal cells. The remainder of the test is crowded with the conspicuously stellate calcareous spicules 0·03–0·04 mm in diameter. The thoraces of the zooids are firmly embedded in the test along their ventral surface. The cloacal canal is fairly restricted and is at thoracic level.

ZOOIDS: These are very small, about 0·7 mm. The branchial aperture is 6–lobed and the atrial opening is wide. There is a large oval lateral organ in the middle of each side of the thorax. There are four rows of only five oval stigmata. The three languets of the dorsal lamina are especially long. There are the usual very fine muscle fibres on the thorax that extend from between the rows of stigmata into two bands in the pharyngeal wall either side of the dorsal lamina and into the short retractor muscle where they are joined by fibres from the outer wall of the atrial cavity.

The abdomina are firmly embedded in the solid basal test. There is a narrow duodenal area. The intestine curves ventrally and to the left before curving dorsally and then anteriorly so that the part of the gut loop distal to the stomach bends ventrally at an angle to the long axis of the zooid. There is conspicuous glandular material in the loop of the gut. The zooids in the colony are not sexually mature.

REMARKS: Owing to the lack of gonads in both recorded specimens, the generic status of this species is unconfirmed. However the oval stigmata, the flat lateral organ and the secondary curve of the gut loop suggest that *Didemnum*, rather than *Lissoclinum*, is the appropriate genus. The small size of the zooid, conspicuously stellate spicules and flat oval lateral organ together with embedded plant cells distinguish this species from other algal containing didemnid species that are presently known.

Trididemnum clinides Kott, 1977
(Figs. 4, 5; Plates 3·1a,b)

Trididemnum clinides Kott, 1977, p. 617.
Trididemnum viride: Tokioka, 1967, p. 87 (part, zooids with atrial siphons).
Trididemnum sp. Eldredge, 1967, p. 184.

MATERIAL EXAMINED

NEW RECORDS: Viti Levu, Fiji, August 1979: Votualailai, under cascades, fringing reef, QM G12620.

PREVIOUSLY RECORDED: *Trididemnum clinides* Kott, 1977, Holotype QM G9928 (with larvae); Paratypes QM G9931. *Trididemnum viride:* Tokioka, 1967, USNM 11646.

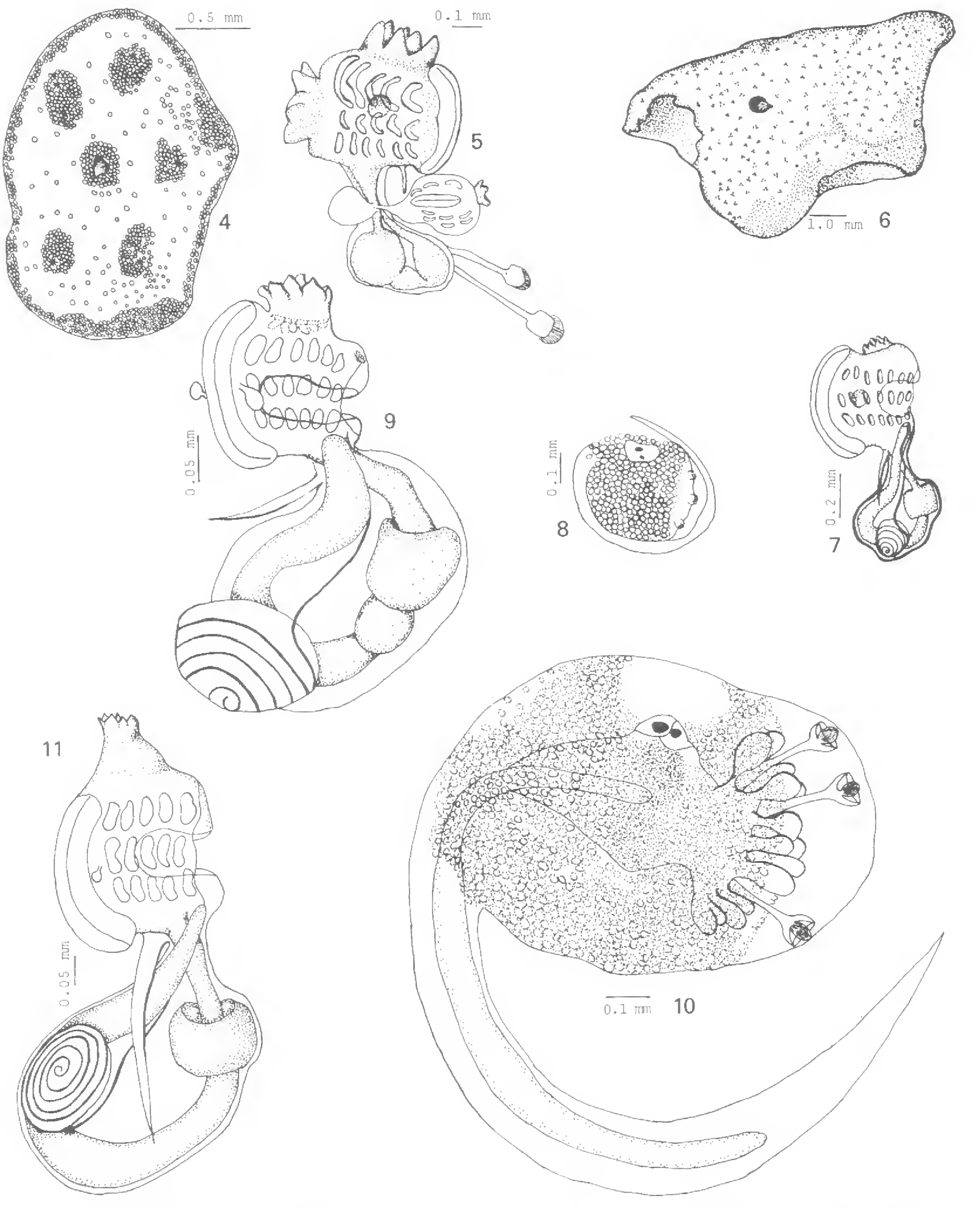
DISTRIBUTION

RANGE: Great Barrier Reef: Heron I. (Kott 1977). Fiji: Votualailai (new record). Philippines (Tokioka 1967). Eniwetok (Eldredge 1967).

HABITAT: At Heron I. the species occurs just below the low tide mark in cryptic habitats near the reef edge and in the lagoon (where it is more common). The Fijian specimens were taken where the water of the fringing reef flat drains into the river channel that bisects it. The colonies are found deep in the dense algal mat that covers the reef beneath these cascades, where a fast unidirectional current flows for about half of each tidal cycle. The Philippine specimens were also taken from shallow water but little other information is available concerning their habitat.

DESCRIPTION

COLONY: The colonies are small, almost spherical or oval or slightly irregular. Large colonies are more or less flattened on the upper surface. The zooids are arranged in a single circle toward the periphery of the colony, and there is a single central common cloacal opening in the centre of the upper surface. The test is very soft. The basal test and sometimes extensions of it attach the colonies to the substrate and they are often difficult to remove. There is a thin superficial layer of bladder cells. Spicules are sometimes but not always, dense in the border and base of the colonies. They are quite sparse in the surface of the colony except where there are dense patches over the anterior end of each zooid. The branchial apertures actually open toward the outer border of each of these patches of spicules. Elsewhere the spicules are evenly distributed and mixed with the algal cells that are embedded throughout the soft test. Algal cells are most



FIGS. 4–5: ***Trididemnum clinides*** (QM G12620) — 4, colony from the upper surface showing distribution of spicules, and branchial and cloacal apertures; 5, zooid with buds and stolonic vesicles (gonads not shown).

FIGS. 6–8: ***Trididemnum miniatum*** (QM G12478) — 6, colony; 7, zooid; 8, larva.

FIGS. 9–10: ***Trididemnum strigosum*** (USNM 11681) — 9, zooid; 10, larva.

FIG. 11: ***Trididemnum nubilum*** (USNM 11641) — zooid.

common in the surface test. The colonies are a pale cloudy mustard green owing to the mixture of spicules and plant cells throughout the test. The common cloacal cavity is thoracic, but rather deep, extending the whole length of the thorax. There are small accumulations of spicules where the atrial openings enter the cloacal cavity. There do not appear to be any plant cells lying free in the common cloacal cavity. Spicules are stellate, from 0·03 to 0·04 mm with a variable number of rounded or conical rays.

ZOOIDS: These are small (about 1 mm). The branchial lobes are deeply incised and there is a conspicuous short, wide atrial siphon with its border produced into six shallow obtuse lobes. There are 3 rows of 5 long rectangular stigmata in each of the 3 rows. There is a rounded lateral organ in the centre of the thorax and a very short retractor muscle. The gut loop is of the usual form with the vas deferens wound 6·5 times around the ♂ follicle. The zooids are colourless but there is often some brown pigment in the test.

LARVAE: These have been taken from specimens collected at Heron I. in January (QM G9922) and in the Philippines in January. They were not present at Votualailai in July. They are 0·6 mm long and the mature larva is enveloped in a dense coat of plant cells that are absent only from areas around the anterior end of the larva to expose the 3 median adhesive papillae, and a circular area over the otolith and ocellus. Ectodermal ampullae are characteristically short and rounded, at either side of the base of the stalks of the adhesive organs.

REMARKS: Tokioka (1967) believed *Didemnum viride* (Herdman, 1906) to be synonymous with a species of the genus *Trididemnum* which has been found to include specimens of the present species. All the species have plant cells embedded in the superficial layer of test. However, the 4 rows of stigmata that is characteristic of the genus *Didemnum* has been confirmed for Herdman's species. *Trididemnum viride:* Tokioka, 1967, includes specimens of *T. miniatum* and two new species of *Trididemnum* in addition to the present species. The possible habitat preferences of *T. miniatum* and the present species are discussed below.

The atrial siphon also distinguishes the present species from *T. cyclops* (which has similar spicules). They are further distinguished by the distribution of spicules, which in *T. cyclops* appear from the surface to be in a dense concentration around each branchial siphon that is continuous with the concentration of spicules around the border of the colony.

Didemnopsis globuliferum Sluiter, 1913, which Tokioka (1967) has suggested as synonymous with his specimens, appears to be a junior synonym of *Trididemnum discrepans* (Sluiter, 1909).

Trididemnum miniatum Kott, 1977
(Figs. 6–8; Plate 3·2)

Trididemnum miniatum Kott, 1977, p. 617.
Trididemnum viride: Tokioka, 1967, p. 8 (part, colonies with smaller spicules).

MATERIAL EXAMINED

NEW RECORDS: Green I.: August, 1979, on seagrass, south of jetty, close inshore (with larvae), QM G12478. Heron I.: October 1979, cryptic near reef edge below LWM (with larvae) QM G12622.

PREVIOUSLY RECORDED: *Trididemnum miniatum* Kott, 1977, Syntypes QM G9927 (with larvae); Paratypes QM G9945. *Trididemnum viride:* Tokioka, 1967, USNM 11661 (part), USNM 11796 (part).

DISTRIBUTION

RANGE: Great Barrier Reef: Heron I. (Kott 1977); Green I. (new record); Philippines (Tokioka 1967).

HABITAT: The species has been taken with *T. cyclops* on coral debris and on weed below the low tide mark in cryptic habitats behind the reef crest and in the lagoon at Heron I. At Green I. however, the species was taken on the sandy inner reef flat, attached to sea grass blades. Philippine specimens are also taken in very shallow water.

DESCRIPTION

COLONY: These are small and rounded to elongate. Some colonies are up to 1·0 cm in their maximum dimension, but more often they are about 4 mm in diameter. They are white to lime green or emerald green depending on the concentration of spicules in the test where they are mixed with algal cells. There are some fine veins of red pigment in the surface test in fresh material. Spicules are either present or absent in the superficial layer of test where the algal cells are most dense, and are quite dense throughout the remainder of the test, providing a white background for the green cells in the surface

layers of the colony that emphasises their colour. Spicules are usually absent from the surface test in the areas just over the zooids, although they are often present in the tips of the branchial lobes. The algal cells become progressively less dense toward the base of the colony where they are absent altogether. They are also present in the common cloacal canal. The spicules are only 0·01 to 0·02 mm, spherical, with numerous blunt ended rays. There is no conspicuous superficial layer of bladder cells in this species. The common cloacal canal is shallow and thoracic. The colonies are attached only lightly to the substrate by strands of test and are easily removed.

ZOOIDS: These are about 0·8 mm long. They are orange in fresh material but become colourless in preservative. The 6 branchial lobes are sharply pointed. The atrial opening is wide and transverse exposing most of the middle portion of the branchial sac. There is a rounded lateral organ half way down the branchial sac. There are 7 longish oval stigmata in each of the three rows. There is a fairly long retractor muscle from the posterior end of the thorax, extending most of the length of the abdomen. The gut loop is of the usual form, and the vas deferens coils 5·5 times around the ♂ follicle.

LARVAE: Larvae are present in most of the colonies that have been collected. They are known to be present from August to January. It is possible that this small and inconspicuous species breeds throughout the year. Mature ♂ gonads were present in the Green I. colonies but not in those from Heron I. in either October or December and it is probable that testes mature before the ovary. The larvae are of the usual *Trididemnum* form with a coat of algal cells present in the mature specimens. This algal coat is interrupted over the otolith and ocellus, and at the anterior end of the larval trunk, exposing the adhesive organs. There are 3 adhesive organs in the median line and 3 pairs of elongate ectodermal ampullae. The larval trunk is 0·7 mm long.

REMARKS: The relatively small spherical spicules and their absence from the test immediately over the anterior end of the zooids helps distinguish this species from two others from the Philippines with which Tokioka (1968) had confused it. All three species have small zooids and algal cells embedded in the test and all lack the atrial siphon of *T. clinides*. The present species often shares a habitat with *T. clinides*. Although both have a wide geographic range that includes the Philippines and the Great Barrier Reef, *T. miniatum* was not taken with *T. clinides* at Votualailai, nor was *T. clinides* taken with *T. miniatum* at Green I. Thus, they may have slightly different ecological requirements, the softer more delicate *T. clinides* possibly being less tolerant of reef flat conditions than the smaller *T. miniatum,* which however, makes a less robust attachment to the substrate than *T. clinides,* and is less often found where strong water flow and turbulence is likely to affect it. Further to the south (at Heron I.) *T. miniatum* is found in the lagoon and near the edge of the reef in cryptic habitats, but not on the sandy inner reef flat where it is found at Green I.

Trididemnum strigosum n. sp.
(Figs. 9, 10; Plate 3·3)

Trididemnum viride: Tokioka, 1967, p. 87 (part, spicules with fewer rays).

MATERIAL EXAMINED

PREVIOUSLY RECORDED: *Trididemnum viride:* Tokioka, 1967, Holotype and Paratypes USNM 11681 (part, with larvae), 11640 (part), 11641 (part), 11642, 11649, 11661 (part), 11672 (part), 11796 (part).

DISTRIBUTION

RANGE: Philippine Is (Tokioka, 1967).

HABITAT: The species has been taken principally on algae and sea grass at depths of 1–6 m.

DESCRIPTION

COLONY: Colonies are very thin investing sheets up to 2 cm in length. They are closely applied to the surface of the substrate, investing weed and sometimes coral fragments, and are consequently very irregular. Sometimes the colonies are elongate and lobulating. The test is densely packed with large stellate spicules, 0·05–0·08 mm in diameter, with 7 conical pointed rays in optical section. The test is brittle and its surface is granular owing to the density of the spicules contained in it. Plant cells are found embedded in the superficial layer of test above the spicules. They are especially small (0·004–0·01 mm). The cloacal cavity is thoracic and very limited. Zooids are evenly spaced, about 1 mm apart, and are seen from the surface as dark points interrupting the spicules.

ZOOIDS: Zooids are extremely small, only about 0·5 mm in total length. The dark pigmentation is usually conspicuous around the branchial aperture. There is a distinct branchial siphon with 6 triangular lobes. The atrial aperture is a transverse incision. There are 3 rows of 7 elongate-oval stigmata. A stalked lateral organ projects outwards from opposite the second row of stigmata on either side of the endostyle. The retractor muscle is of moderate length. The gut loop is fairly long, and flexed ventrally with a distinct right-angle bend in the rectum where it extends anteriorly. The ♂ follicle is deep and with 5·5 coils of the vas deferens.

LARVAE: Larvae are present in the colonies from Basilau I. in January. They lie in the test where they become surrounded by a capsule of plant cells that become embedded in the larval test. They are about 1·1 mm long with a short tail extending only half way around the larval trunk. There are 6 to 8 pairs of ectodermal ampullae that arise from the frontal area around the stalks of the three adhesive organs. The variation in the number of ectodermal ampullae is caused by their subdivision. The frontal area is separated from the central area of the larval trunk where the developing oozooid expands. The posterior haemocoelic chamber tapers posteriorly around the base of the tail. The plant cells embedded deep in the larval test are absent only from the area over the sense organs and anteriorly in front of the adhesive apparatus. As the oozooid swells in the centre of the larval trunk, the test and its contained plant cells becomes thinner in this area and the developing oozooid can be seen.

REMARKS: The zooid of the present species resembles that of *T. miniatum*, although it is even smaller. The species is distinguished by its very large and dense stellate spicules, and its large larva with embedded plant cells. The thin investing colonies are also characteristic.

Trididemnum nubilum n. sp.

(Fig. 11; Plate 3·4)

Trididemnum viride: Tokioka, 1967, p. 87 (part, specimens with numerous rays).

MATERIAL EXAMINED

PREVIOUSLY RECORDED: *Trididemnum viride:* Tokioka, 1967, Holotype and Paratypes USNM 11641, 11640 (part), 11659 (part), 11661 (part), 11672 (part), 11680, 11681 (part), 11796 (part).

DISTRIBUTION

RANGE: Philippine Is. (Tokioka 1967).

HABITAT: The habitat is apparently the same as that of the previous species, and is found on weed, in shallow water, and on or in the vicinity of coral reefs.

DESCRIPTION

COLONY: The colonies are small and irregular but rather solid. The spicules are evenly spaced in the solid gelatinous test which is translucent and a slightly pink-brown colour in preservative. Spicules are seldom dense in any part of the test and sometimes they are sparse in the middle layers of test. The spicules are large (0·03–0·05 mm diameter). They are almost spherical, with about 10–14 short pointed rays in optical section. There are occasional spicules with blunt rays. The plant cells are slightly larger than those of *T. strigosum* (about 0·015 m diameter). They are mixed with the spicules in the upper layer of test, above the common cloacal cavity. It is this mixture of spicules, plant cells and test that confer the rather fluffy, soft appearance to the colony that is also reminiscent of *T. clinides*.

ZOOIDS: Zooids are evenly spaced in the colony and are sometimes brown in the preserved specimens. They are small, about 0·6 mm in total length. The branchial lobes are minute, the atrial aperture is a deep transverse incision and there is a conspicuous flat circular mass of spicules in the lateral organ which projects outwards on either side of the endostyle. There are three rows of 5 elongate-oval stigmata. The retractor muscle is strong and is sometimes very long. The gut forms a simple horizontal loop and the single ♂ follicle with 5·5 coils of the vas deferens, is rather flat in comparison with *T. strigosum*. Testes were mature in most of the colonies but no larvae were found.

REMARKS: This species with its incised atrial aperture, very small zooids and embedded plant cells, is distinguished from *T. miniatum* and *T. strigosum* by its large, almost spherical spicules, strong retractor muscle, and tough gelatinous test and translucent appearance. *T. clinides* resembles the present species in external appearance but is readily distinguished by its atrial aperture, larger zooids and smaller stellate spicules with fewer rays. The spicules resemble those of *T. paracyclops* but in the latter species zooids are larger and plant cells are confined to the common cloacal cavity.

Tridideminum cyclops Michaelsen, 1921
(Figs. 12–14; Plates 4·1 a,b)

Trididemnum cyclops Michaelsen, 1921, p. 19. Hastings, 1931, p. 89 Kott, 1962, p. 581; 1966, p. 286; 1977 (part), p. 616. Eldredge, 1967, p. 183. Tokioka, 1967, p. 85 (part). Thorne, Newcomb and Osmond, 1977, p. 575.

Not *T. cyclops* Newcomb and Pugh, 1975 p. 534 (< *Didemnum* sp.)

Lissoclinum pulvinum: Tokioka, 1967, p. 97 (part).

MATERIAL EXAMINED

NEW RECORDS: Fiji (Viti Levu) fringing reefs, July 1979: Vuda Point, in pools below the low water mark, outer reef flat, QM G12453 (some larvae); Tailevu, amongst living coral at low water mark on reef edge, QM G12455; Makaluva reef, in pools at low water outer reef flat, QM G12460. Fiji (Viti Levu), fringing reefs, August 1979: Votualailai, beneath cascades tangled in algal mat, QM G12619.

PREVIOUSLY RECORDED: *Trididemnum cyclops* Michaelsen, 1921, Syntypes, ZMH K1110; Tokioka, 1967, USNM 11482, 11483; Kott, 1977, QM G9942 (with larvae), G9944. *T. viride:* Tokioka, 1967, USNM 11661 (part). *Lissoclinum pulvinum* Tokioka, 1967, USNM 11480 (part), 11643 (part), 11684 (part), 11669 (part).

DISTRIBUTION

RANGE: Malagasy (Michaelsen 1921). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Hastings 1931, Kott 1977). Philippines (Tokioka 1967). Gilbert I. (Tokioka 1967). Fiji: Viti Levu (new record). Eniwetok (Eldredge 1967).

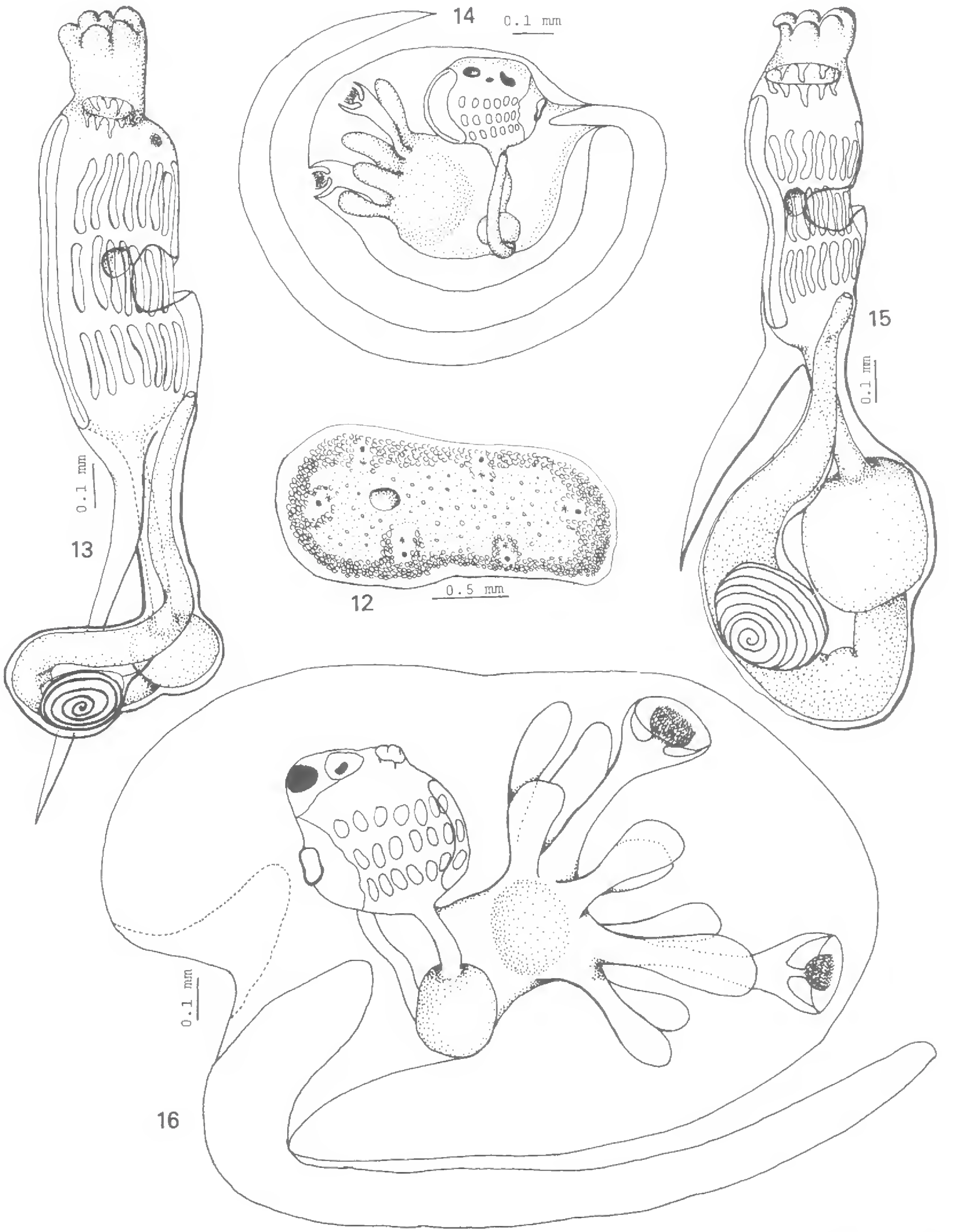
HABITAT: The species lives in cryptic habitats on weed, coral and rocks just below the low water mark in pools behind the reef crest and in the lagoon, and between coral branches and in the interstices of algal mats at the reef edge. It is a common species but is found generally where water flow is not strong, or in habitats where it is well protected, and usually where it is well shaded. It is often found with *Lissoclinum bistratum* and *T. miniatum*. With *Trididemnum miniatum* and *Diplosoma virens* it is found in deeper and less exposed locations at Heron I. than at locations further to the north.

DESCRIPTION

COLONY: These are characteristically small and oval, usually less than 1 cm in length. Dense spicules line the borders and base and there is a thick superficial layer of bladder cells that surround the colony, usually extending around onto the base. This bladder cell layer is less dense on the upper surface. The spicules are usually absent from the upper surface, which is green owing to the plant cells in the thoracic common cloacal cavity. There is usually a single system in each colony, with a central, sessile cloacal aperture. Colonies appear to divide when they exceed 0·5 cm in length. A constriction in the border eventually spreads across the surface and divides the colony from the surface toward the base (see specimens QM G12453, Vuda Point, Viti Levu, July, 1979). The zooids are arranged around the border, their ventral surface embedded in the test. The presence of the zooids around the circumference of the colony creates their characteristic surface appearance. Each whitish zooid projects into the green algal-filled cloacal cavity from the white spicule-filled border of the colony. The dark endostylar pigment cap is visible on the anterior surface of each of the zooids. There may be a single layer of spicules, of varying concentrations over the remainder of the surface test beneath the bladder cell layer. The spicules are fairly dense in a layer beneath the shallow thoracic common cloacal cavity but become less dense toward the base of the colony. There are 0·03–0·04 mm in diameter with some at 0·06 mm. There are two types of spicules, the most numerous with about 12–14 conical pointed rays in optical cross section. There are also spicules with more numerous, almost parallel sided rays.

ZOOIDS: These are almost 1·5 mm long when extended. The branchial aperture has 6 pointed, deeply divided triangular lobes. The atrial aperture is a deeply incut opening. There are 7 long oval stigmata in each of the three rows. The retractor muscle is long and broad where it arises from the neck of the zooid. The abdomina are embedded in basal test and are only about one quarter of the length of the thorax. The gut loop is flexed ventrally. The vas deferens coils 5·5 times in an anti-clockwise direction around the ♂ follicle.

LARVAE: Although they are present in colonies from Viti Levu in July, the more prolific colonies were those from Heron I. lagoon in December 1976 (QM G9942), and from Keeper Reef off Townsville in August 1977. In some colonies mature eggs and larvae are present but ♂ glands appear to be spent suggesting their earlier maturation. The species may breed throughout the year, with a peak in larval production in the summer months. Mature embryos are 0·5 mm long. They begin their development in the basal



FIGS. 12–14: *Trididemnum cyclops* (QM G9942) — 12, colony showing endostylar pigment caps and distribution of spicules beneath the superficial bladder cell layer; 13, zooid; 14, larva.

FIGS. 15–16: *Trididemnum paracyclops* (QM G12628) — 15, zooid; 16, larva.

test and subsequently move into the common cloacal cavity where they acquire a coating of plant cells that is interrupted over the sense cells and around the front of the larval body to expose the two adhesive organs. The tail is stout and is wound three quarters of the way around the larval trunk. There are two pairs of ectodermal ampullae and the characteristic two adhesive organs.

REMARKS: The species is distinguished by the size of the colonies, by the single systems in which zooid are restricted to the border of the colony. The solid translucent superfical layer of bladder cells and the endostylar pigment cap occur in a related species of this genus (see below) which is distinguished by the size of the colony, a relatively large abdomen and greater number of vas deferens coils and the size of the larva and the number and modification of its ectodermal ampullae.

Trididemnum paracyclops n. sp.
(Figs. 15, 16; Plates 4·2 a,b)

Trididemnum spiculatum Kott, 1962, p. 281 (part, specimen from Heron I.).
Trididemnum cyclops: Kott, 1977, p. 47 (part, extensive sheets).

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic habitats in pools behind reef crest, Holotype QM G12627, Paratypes QM G12628 (with larvae).

PREVIOUSLY RECORDED: *Trididemnum cyclops:* Kott, 1977, QM G9446, G9788, G9909, G9910, G9912, G9915, G9916, G9917, G9918, G9940, G9941 (with larvae), G9943 (with larvae), G12630 (with larvae). *Trididemnum spiculatum* Kott, 1962 (part, specimen from Heron I.), AM Y1627.

DISTRIBUTION

RANGE: Great Barrier Reef (Lizard I. to Heron I.). It has been recorded principally from Heron I. where it appears to be very common but is also present amongst the specimens previously identified as *T. cyclops* (Kott 1977) from Lizard I. (QM G9912), Nymph I. (QM G9788), Wilson I. (QM G9940) and Northwest I. (QM G9917).

HABITAT: The species is found investing dead coral (*Acropora*) branches and rock in shaded cryptic habitats below the LWM, in deeper pools behind the reef crest.

DESCRIPTION

COLONY: Extensive and irregular investing sheets, up to 5 cm in greatest dimension and 2·3 mm thick. In one colony (QM G9943) a strip of the colony has overgrown the surface and fused with another part of the colony. This is a simple example of the phenomenon which, in *Trididemnum cerebriforme*, creates a most complex pattern. There is a superficial layer of bladder cells which surround the colony, extending around the border and onto its lower surface. In the border of the colony the spicules are fairly dense beneath this bladder cell layer. They are of variable, though even, density in the upper surface. The green colour of the colony is a result of the green plant cells seen through the surface test and it varies with the density of the white spicules in the surface layer of test. There is a dense layer of spicules below the shallow thoracic cloacal cavity (in which the algal cells occur) and beneath this they are absent altogether except for a single layer which is sometimes present where the test is attached to the substrate. Dark pigment occurs in the basal layer of test and sometimes in the zooids and this pigment often stains the preserving fluid most conspicuously. The spicules are large, from 0·03 mm to almost 0·08 mm. They are all of the one type with about 14 conical rays in optical transverse section.

Zooids are evenly and quite densely distributed in the colony. Sometimes the peripheral zooids are embedded in the test of the border of the colony, as in *T. cyclops,* but more often the cloacal cavity extends around between the border and the zooids, which appear, from the surface, to be surrounded by a thin layer of spicules (contained in the thoracic test sheath) and the green cells within the cloacal cavity. The zooids can be observed through the surface test, although they are not as conspicuous as in *T. cyclops*. Small colonies differ from *T. cyclops* in the large number of zooids which are crowded evenly in the colony and not just arranged around the periphery and the endostylar pigment cap is not always visible from the surface in the present species.

ZOOIDS: These are about 1·5 mm long when fully extended. The branchial lobes are fairly shallow. The atrial aperture is deeply incised. There are 7 stigmata in each of the three rows. The retractor muscle is relatively short and broad and does not extend beyond the abdomen. The abdomen is almost the same size as the thorax. The gut loop is fairly straight and is not flexed ventrally. There is a very large ♂ follicle with the vas deferens wound anti-clockwise 9·5 times around it.

LARVAE: Although most of the specimens collected are fairly robust, larvae are only present in small numbers in colonies collected in October

and December. They are not present in colonies taken in August, September, January and March at Heron Island, nor in the Nymph I. specimens in June. Mature ♂ follicles are present in colonies collected in October. The available data suggest a restricted breeding period in early summer (October to December). The larvae are exceptionally large, with a body 1 mm long, the tail wound only half way around. There are only two adhesive organs but there are four pairs of ectodermal ampullae and an additional unpaired dorsal one. The plant cells do not form a coat around the larva as in other species in this genus but are attached to an area at the posterior end of the body where the posterior haemocoelic chamber is extended around the base of the tail. The algal cells adhere to the larval test either side of the mid line. As the tail straightens, its proximal end, in the posterior haemocoelic chamber, is drawn down and a pocket develops just above it in the postero dorsal part of the larval test. The plant cells that adhere to this part of the larval test are accordingly enclosed in an incipient cloacal cavity that, in due course, receives the atrial openings of the zooids that surround it. The larvae are apparently free swimming for a very limited period and a larva has been observed in which the tail is in the process of resorption in the posterior haemocoelic chamber before the larva is released from the cloacal cavity. A round yolk mass persists until a late stage in the elongate frontal section of the larva.

REMARKS: The species was formerly thought to represent large colonies of *T. cyclops*. The larvae are almost twice the size of those of *T. cyclops*, they have more ectodermal ampullae, and the plant cells are differently distributed on them. Closer examination of both species has demonstrated differences in the colony, the spicules, the proportions of the zooids and their retractor muscles, the course of the gut, and the number of vas deferens coils.

It is also possible that colonies of *T. cyclops* lobulate when they reach a certain size while in *T. paracyclops* neither the size of the colony nor the number of zooids and systems in it are restricted in this way. The species is distinguished from *T. natalense* and *T. savignyii* by the absence of an atrial siphon and the presence of only two larval adhesive organs.

Lissoclinum voeltzkowi (Michaelsen, 1920)
(Figs. 17–19; Plates 1·3a,b and 1·4)

Didemnum voeltzkowi Michaelsen, 1920, p. 54. Hastings, 1931, p. 97.

MATERIAL EXAMINED

NEW RECORDS: Heron I.: March 1975, under rocks, rubble zone, near eastern end of south reef, QM G12633; December 1976, under rocks, rubble zone, eastern end of south reef; QM G12632. Green I.: August 1979, inner sandy reef flat, on brown algae, QM G12474 (with larvae). Lizard I.: June 1976, blue lagoon, on coral in shallow water, low tide, QM G9913, G12621 (with larvae). Fiji (Viti Levu) July 1978: Malevu, fringing reef, sandy reef flat, QM G12479 (with larvae); Suva Barrier Reef, sandy reef flat, G12472 (with larvae); Makaluva reef, sandy reef flat, G12473 (with larvae). Fiji (Viti Levu) August 1979: Votualailai under cascades in interstices of algal mat QM G12617. Philippines: Van Name *det.* AMNH Chordata 2128.

PREVIOUSLY RECORDED: *Didemnum voeltzkowi* Michaelsen, 1920, Types ZMH K1099, K1111; Hastings, 1931, BM 30.12.17.44 (one colony in the Australian Museum, Sydney), BM 30.12.17.43.

DISTRIBUTION

RANGE: Malagasy (Michaelsen 1920). Great Barrier Reef: Low Is. (Hastings 1931); Green I. and Heron I. (new records). Fiji: Viti Levu (new records). Philippines (new record).

HABITAT: The habitat requirements of this species are possibly the most restricted of all the plant-bearing didemnid species (with the exception only of the endemic diplosomid from Viti Levu). They are found near the low tide mark, on the outer part of the open sandy reef flat. They are not normally cryptic. They often occur on weed (including *Halimeda*). On the fringing reefs of the Fijian island of Viti Levu a mosaic of colonies of this species, each colony contiguous along its borders with adjacent colonies, covers vast areas of the sandy reef flat inshore from the living coral zone. They were absent only from the northern fringing reefs at Tai Levu. On the Great Barrier Reef at Green I. the species is also found in abundance inshore from the living coral zone of the reef flat although at this location it is attached to sea-weed and is not lying on the sandy sediments. At Heron I. the relatively small number of small colonies are from the rubble zone near the reef edge at the eastern end of the reef, and at one location on the southern edge of the reef.

DESCRIPTION

COLONY: The living colonies are a dirty greyish brown or cream or greenish cream with dense brown-black pigment contained in spherical cells that are scattered in the surface test and also gathered into small evenly spaced patches between the zooids around the edge of the colony and

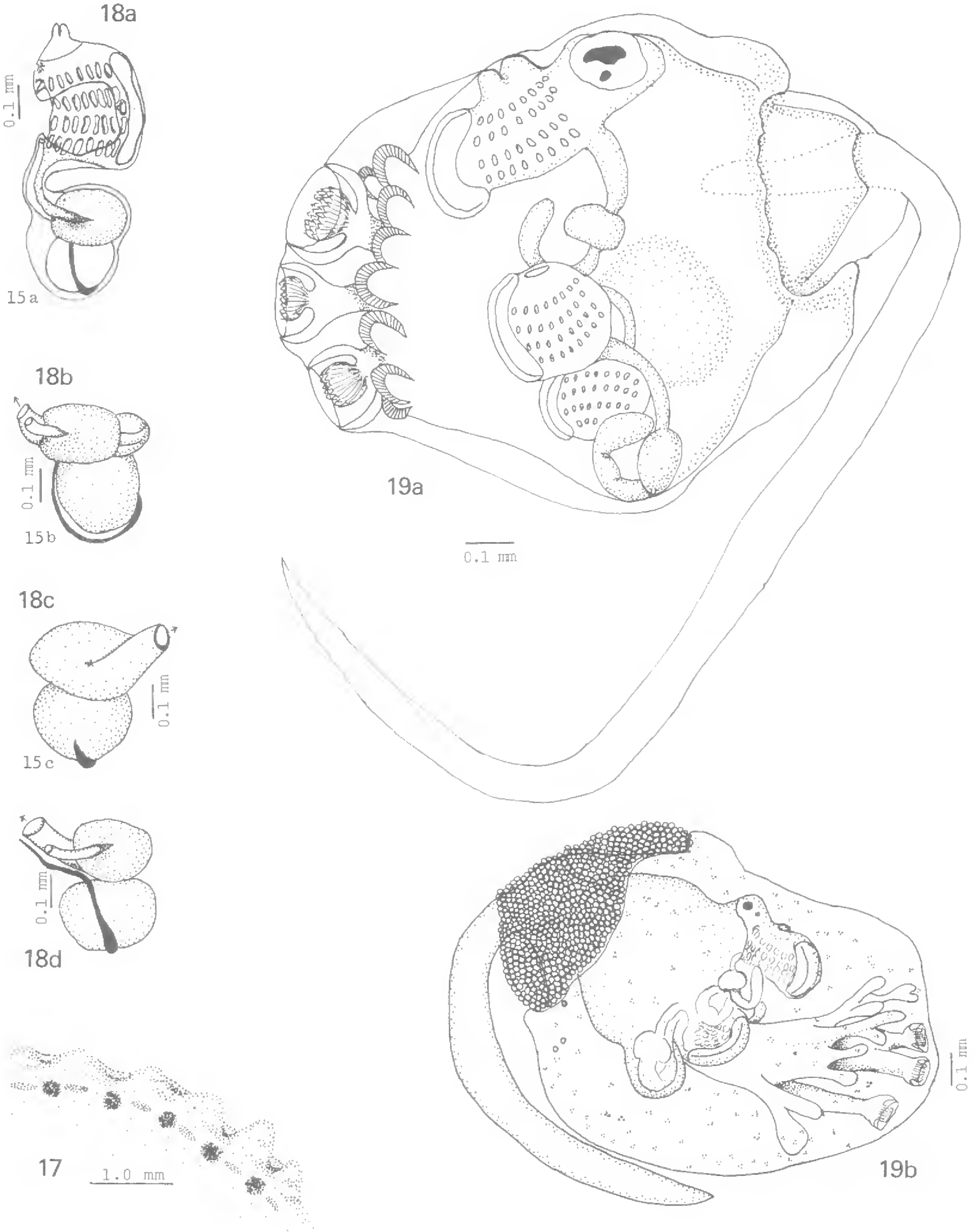
between papillae. Colonies are circular, oval or polygonal flattened cushions up to 4 cm in greatest dimension and up to 5 mm thick. Some of the smaller living colonies appear almost spherical. The borders of the colony are rounded and the test around the periphery of the upper surface is produced into pointed spicule filled conical papillae just outside the peripheral zooid openings. There are occasionally similar papillae from other parts of the upper surface (especially in the colonies from Green I.). The colonies are only loosely attached to the substrate by the basal test. When removed from the substrate the upper surface is depressed and the whole colony seems to contract, the border is elevated and the conical projections around the upper surface become more conspicuous. The colonies from Heron Island are less robust than others, the spicules are relatively sparse in the surface test and it is not produced into conical papillae.

There are one or two cloacal apertures on short tubular projections in the centre of the upper surface. These are made conspicuous by the dense brown pigment in the surrounding test. The branchial apertures are short slits and those around the border are aligned parallel to it. In preserved material these slits are conspicuously green owing to the plant cells that crowd around the branchial sac where it is exposed to the cloacal cavity. Spicules are stellate with 8–12 conical or blunt ended rays in optical section. They are 0·02–0·04 mm in diameter. They are crowded always in the border and in the base of the colony, and usually they are crowded in the surface test and in the test strands that enclose the zooids. In those specimens that are in shaded positions, however, the surface layer of spicules is not dense and the surface of the colony is green owing to green cells in the common cloaca which can be seen through the surface test. Spicules are absent from the area surrounding the cloacal apertures. Cloacal canals perforate the upper layer of test in which the zooids are embedded, and are continuous with voluminous spaces posterior to the zooids.

ZOOIDS: These are crowded in the test. They are about 0·8 mm long. The branchial lobes are reduced to a ventral and dorsal lip and the aperture is a slit. The atrial aperture is wide exposing much of the branchial sac. There are four rows of 8 longish oval stigmata. A deep egg shaped lateral organ projects into the peribranchial space opposite the third row of stigmata at either side of the endostyle. Its attachment to the body wall is narrow so that in section it is comma shaped (Michaelsen 1920). Some very fine muscle fibres extend from the posterior end of the zooid and into the test but these are most inconspicuous and no actual retractor muscle can be demonstrated. The gut loop is short and horizontal. The ♂ gland is undivided and the vas deferens is hooked around it, the proximal end of the duct extending posteriorly from the left side of the follicle, postero-ventrally, and around onto the opposite side where it runs anteriorly along the inner side of the rectum.

LARVAE: These are present in specimens from Fiji in July and a few were present in colonies from Lizard I. on June 1973 (G9913). They were not present in specimens from Green I. (August 1979). Testis follicles appear mature in most specimens. The body of the larva is 1·5 mm long and the short tail is wound only about one third of the distance around it. There are usually three large adhesive organs, rather close together. However, one of these appears to have arisen by subdivision since the two uppermost organs share a basal common stalk. There is a ring of 8 pairs of ampullae around the stalks of the adhesive organs, each with a cap of modified columnar cells. The body of the mature larva contains an oozooid with otolith and ocellus, and two blastozooids. The larval test contains scattered patches of brown pigment cells that are absent only from the area around the posterior end of the body at the base of the tail, where a cap of plant cells adheres in the mature larva. As the larva matures the test appears to be growing back to enclose the posterior end of the larva, together with its adherent plant cells, in a pocket around the base of the tail, that is very likely an incipient cloacal cavity.

REMARKS: Some of the smaller almost spherical living colonies of this species bear a superficial resemblance to *Didemnum molle* in shape and colour. However the cloacal cavity is not so extensive, they lack the copious mucous secretion of *D. molle,* the spicules are relatively large and stellate and the arrangement of pigment, and the conical projections around the border of the colony distinguish them. Those green colonies with less dense spicules in the upper surface are readily distinguished from *L. bistratum* by the form of the spicules and usually by the large spherical pigment cells. The modification of the branchial lobes is also found in *Lissoclinum bistratum* and *L. patellum.*



FIGS. 17–19: *Lissoclinum voeltzkowi* (QM G12474) — 17, part of the border of a colony showing pigment patches (dark shading), branchial apertures, and conical papillae around the borders of the colony; 18, zooid (a, abdomen and thorax; b-d, gut loop and testis from the right, the left, and dorsally, respectively); 19, larva (a, showing test extending posteriorly over area where plant cells are present; b, later larva showing cap of plant cells and pigment patches on test).

Hastings (1931) apparently accepted Michaelsen's interpretation of relationship of the vas deferens in this species with the characteristic spiral duct of the genus *Didemnum*. However its course is characteristic of *Lissoclinum* and is hooked around the posterior border of the gland from the ventral side (against the gut loop) and onto the opposite or dorsal surface. In the genus *Didemnum* the origin of the duct is from the centre of gland on the opposite side.

Both the habitat the appearance of this species over most of its range is most characteristic. Specimens from Heron I. however are few and these have been taken only from cryptic habitats near the eastern end of the reef. Heron I. is possibly at the southern end of the range for the species. The density of spicules in the surface test of these specimens is also much less than most of the specimens further north. The spicules of the surface test undoubtedly protect the colonies from the direct sunlight of the reef flat. Those colonies that occur in shade, or even those parts of a colony that may be curved around the side of a rock into a shaded part of its surface, like the cryptic Heron I. colonies, have fewer spicules in the surface test so that the green plant cells in the cloacal cavity are fully exposed to the light. Light is therefore, possibly an important environmental parameter for this species. Either this factor, or the diurnal temperature range on the reef flat, may preclude its occurrence on the reef flats at the southern end of the Great Barrier Reef.

Lissoclinum bistratum (Sluiter, 1905)
(Figs. 20, 21; Plates 2·1a,b)

Didemnum bistratum Sluiter, 1905a, p. 103; 1905b, p. 18; 1909, p. 46. Hartmeyer 1909, p. 1449. Michaelsen, 1920, p. 48.
Didemnum gottschaldti Tokioka, 1950, p. 118.
Lissoclinum pulvinum Tokioka, 1954, p. 247; 1967, p. 97 (part).
Leptoclinum molle: Kott, 1962, p. 309; 1966, p. 30.
Lissoclinum molle: Tokioka, 1967, p. 95. Kott, 1977, p. 618.
Didemnum patella: Millar, 1963, p. 701.
Didemnum chartaceum: Kott, 1962, p. 324.

Material Examined

New Records: Heron I.: October 1979, below low tide amongst rubble near reef edge, QM G12626 (with larvae). SE. Queensland September 1977: Mooloolabah, 18 m on reef slope QM G10108; Mudjimbah, 17 m on reef slope, QM G10125. Green I.: August 1979, rubble zone, QM G12481. Coral Sea (Marion Reef): August 1977, 8 m on top of reef, QM G10170 (AMPI ascidian 204). Fiji (Viti Levu) July 1979: Suva Barrier Reef, in rock pools outer reef flat, LWM, QM G12466; Makaluva, fringing reef, in pools outer reef flat, LWN, QM G12464; Malevu fringing reef, in pools outer reef flat, QM G12467; Tai levu, fringing reef, in pools amongst coral near reef edge, LWM, QM G12483; Deuba, fringing reef, amongst living coral near reef edge, LWM, QM G12581. Palau Is., LWM, QM G12676.

Previously Recorded: *Didemnum bistratum:* Michaelsen, 1920, ZMH K1607, K1108. *Lissoclinum pulvinum:* Tokioka, 1967, USNM 11386, 11396, 11480 (part), 11487, 11538, 11643 (part), 11647, 11663 (part), 11684 (part), 11669 (part), 11678 (part). *Lissoclinum bistratum* > *L. molle:* Kott, 1977, QM G9908 (with larvae), G9911, G9948, G9949 (with larvae), G9950, G9951 (with larvae), G9952.

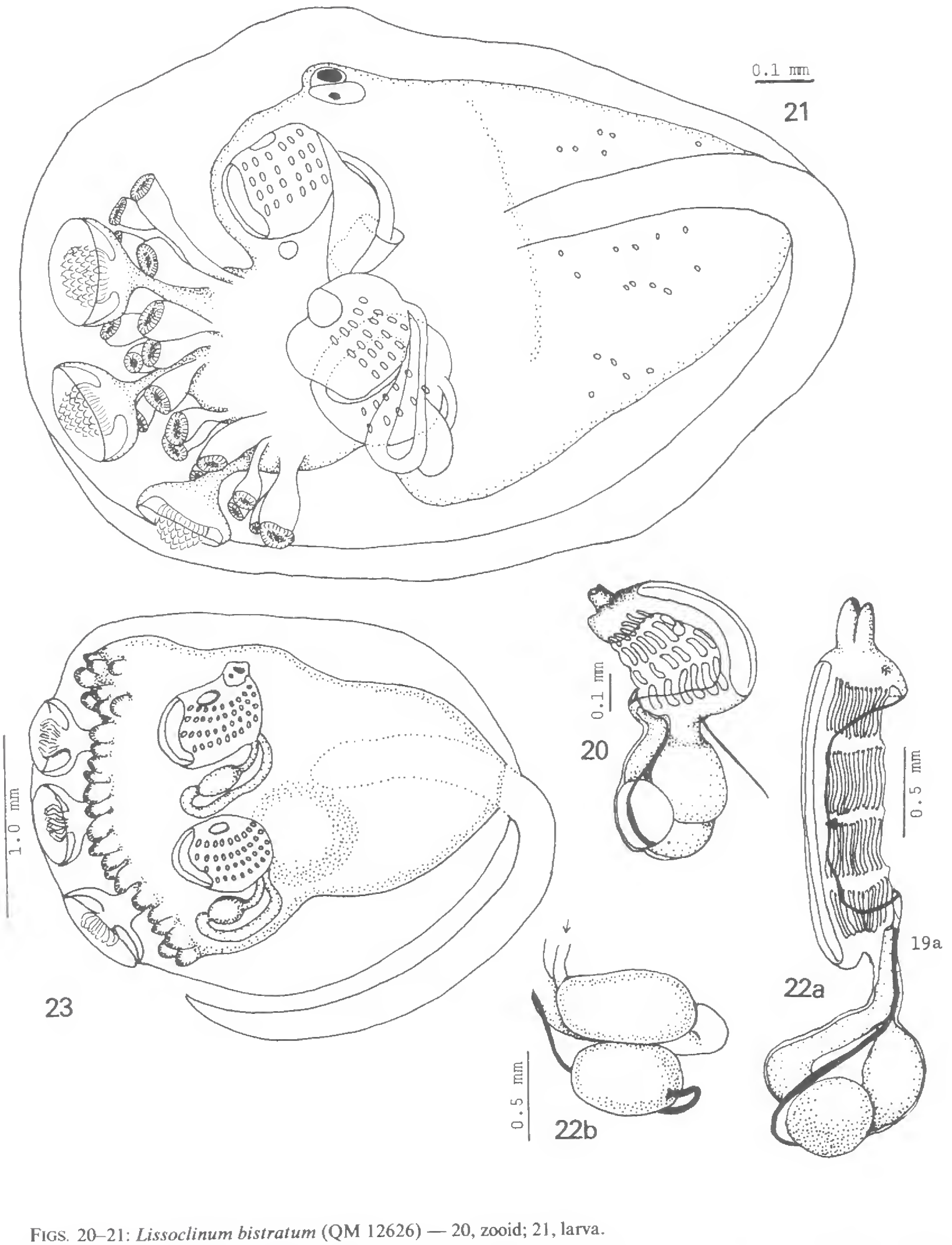
Distribution

Range: Gulf of Aden (Sluiter 1905a, 1905b). Red Sea (Michaelsen 1920). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Millar 1963; Kott 1962, 1977). SE. Queensland (new records). Indonesia (Sluiter 1909). Japan: Tokara Is (Tokioka 1967). Palau Is (Tokioka 1950). Fiji: Viti Levu (new records).

Habitat: The species is taken in cryptic habitats with *T. cyclops* from just below the low water mark in the outer reef flat and in the rubble zone behind the reef crest. Macroscopically it resembled *T. cyclops,* with which it is often confused.

Description

Colony: The colonies are small oval cushions or irregular investing sheets, never more than 5 mm thick. They seldom exceed 2 cm, but sometimes are as much as 5 cm in length (specimens from Mooloolaba QM G10108, G10125). Sometimes the common cloacal aperture is sessile, but it is often raised off the surface of the colony on a cylindrical projection, which may lie over the surface, presumably in the direction of the current flow (see Tokioka 1967). They are grey green on the upper surface. The green plant cells in the common cloacal cavity are visible through the surface test. There is usually a layer of bladder cells superficially. Spicules are dense in the borders, and in the basal test. They are often less dense at the level of the abdomina.



FIGS. 20–21: *Lissoclinum bistratum* (QM 12626) — 20, zooid; 21, larva.

FIGS. 22–23: *Lissoclinum patellum* (QM G9930, zooid; AM Y1335, larva) — 22, zooid (a, from the left latero-dorsal aspect; b, abdomen from the right); 23, larva.

Spicules are evenly distributed in the surface test beneath the bladder cell layer, but their concentration varies from colony to colony and in some specimens they completely occlude the bladder cell layer. There are usually spicules associated with the branchial openings and when the zooids are contracted these are drawn down into the branchial siphon in a thick plug. The spicules are 0·03–0·05 mm in diameter. They are spherical, with many crowded blunt ended rays. The test is relatively delicate in this species. Black or reddish pigment is present in the bladder cell layer and sometimes in the body walls of the zooids. Zooids are most often white with a yellow stomach. The branchial lobes are reduced to a ventral and a dorsal lobe and the apertures appear as slits on the surface of the colony as in *L. voeltzkowi*. The zooids are surrounded by thoracic common cloacal cavities which connect with posterior abdominal spaces, although these are often quite restricted. The basal test is relatively thick.

ZOOIDS: These are about 0·9 mm long. The atrial aperture is wide and open exposing most of the branchial sac. There is a deep vertical egg shaped lateral organ projecting into the peribranchial cavity on either side of the endostyle (near the border of the atrial aperture), between the second and third rows of stigmata. There are 6 to 8 long and rectangular stigmata in each row. The gut loop is simple and vertical. The ♂ gland is undivided and the vas deferens is hooked around the posterior end of the gland.

LARVAE: These are present in colonies from Darwin in October 1965 and from Heron I. in December (QM G9951), January 1976 (QM G9949), March 1975 (G9908 and October 1979 (QM G12626). Colonies from Fiji had some large eggs but no embryos in July (G12581). The species may breed all the year with a peak in early summer.

The large body is about 1 mm long the tail is wound half way around it. There are 3 large adhesive organs surrounded basally by 8 pairs of ectodermal ampullae. There is an oozooid and two blastozooids. The 'pouch' referred to by Kott (1977) is actually the posterior extension of the posterior haemocoelic cavity, with a layer of ectoderm and test outside it. The posterior cap of algal cells adhere to the larval test in this region to form the posterior cap, around the base of the tail described by Kott *(loc. cit.)*. The cells at tips of the 8 pairs of conspicuous ectodermal ampullae are modified columnar cells and form a concavity on the end of each ampulla.

REMARKS: The species is very closely related to *L. voeltzkowi*, which has a similar (though more extensive) cloacal cavity, similar zooids, lateral organ, branchial sac, gut loop, and larva. In its more characteristic form the colony of *L. voeltzkowi* is readily distinguished from *L. bistratum*. However in cases where spicules are not dense in the surface test of *L. voeltzkowi* or when they are dense in the surface test of *L. bistratum* the spicules constitute a reliable means to distinguish the species.

This species has been reported further to the south than has so far been recorded for any other algal-bearing didemnid.

Lissoclinum patellum (Gottschaldt, 1898)
(Figs. 22, 23; Plate 2·2)

Didemnoides patella Gottschaldt, 1898, p. 653.
Didemnoides sulcatum Gottschaldt, 1898, p. 651.
Didemnoides ternatanum Gottschaldt, 1898, p. 648.
Didemnum patella: Michaelsen, 1920, p. 63. Tokioka, 1950, p. 115. Millar 1975, p. 228.
Leptoclinum patella: Kott, 1962, p. 310.
Lissoclinum patella: Tokioka, 1967, p. 97. Kott, 1977, p. 619.
Diplosomoides tropicum Sluiter, 1909, p. 88.
Didemnum meandrium Sluiter, 1909, p. 64.
Not *Didemnum ternatanum:* Kott, 1977, p. 618 and synonyms (< *D. molle).*
Not *Didemnum patella:* Millar, 1963, p. 701 (< *L. bistratum).*

MATERIAL EXAMINED

NEW RECORDS: Swain Reefs: October 1974, reef slope, QM G9930. Heron I.: November 1978, reef slope, QM G1190. Palau Is., QM G12679.

PREVIOUSLY RECORDED: *Didemnoides patella* Gottschaldt, 1898, Holotype ZMH K1087. *Lissoclinum patella:* Tokioka, 1967, USNM 11419, 11637, 11664, 11688; Kott, 1962, AM Y1335 (with larvae); 1977, QM G9278, G9456, G9887. *Didemnoides ternatanum* Gottschaldt, 1898, Holotype ZMH 595. *Lissoclinum tropicum:* Van Name det., AMNH Chordata 2143. *Didemnum maeandrium* Sluiter, 1909, Syntypes ZMA TU.459, TU.457.

DISTRIBUTION

RANGE: Western Australia: Pt. Peron, Rottnest I. (Kott 1962). Great Barrier Reef: Heron I., Swain Reefs (Kott 1962, 1977). Indonesia (Gottschaldt 1898, Sluiter 1909, Millar 1975). Borneo (Sluiter 1909). Palau Is. (Tokioka 1950, 1967).

HABITAT: The species is one of the few plant bearing didemnids that does not occur intertidally. It is taken on vertical surface and under ledges from very shallow water to about 10 m. Larger specimens are taken only from deeper water. The species is large and robust and it is unlikely that adequate attachment to the substrate could be effected unless the substrate was free of sediments.

DESCRIPTION

COLONY: Large colonies up to 1 cm in thickness. They have firm rounded gelatinous ridges on the surface. Cloacal and zooid openings are between these ridges. The basal test is also firm and gelatinous and as thick as the surface ridges. Small colonies consist of a single system that is surrounded by a ridge of gelatinous test around a central depressed area. Subsequently raised surface swellings develop (Tokioka 1967) and in due course assume the characteristic facies of the larger colonies (see Millar 1975, fig. 20). The thin zooid layer is conspicuous owing to the plant cells that fill the common cloacal cavity that surrounds the zooids and extends posterior to them. Spicules are also present in the zooid layer of test. They are characteristically spherical, and have a large size range, from 0·01 to 0·08 mm in diameter.

ZOOIDS: These are large. There are 4 rows of 14 very elongate stigmata. There are very fine muscle fibres in the transverse vessels that fan out either side of the endostyle and form circular bands around each zooid. There do not appear to be any longitudinal fibres along the dorsal or ventral borders of the pharynx and there is no retractor muscle. The long rectangular stigmata are almost completely exposed and the peribranchial cavity is almost completely lost, a narrow strip along either side of the endostyle being all that remains of the outer body wall. There is a small egg-shaped lateral organ projecting inwards between the second and third rows of stigmata. The two lobes of the branchial siphon, each with longitudinal muscle fibres that curve toward each other in the border, are marked by clumps of spicules where they are inserted into pockets of test. The oesophagus is long and the stomach and intestine form a simple loop that is flexed ventrally at an angle to the thorax. The single egg shaped ♂ follicle lies in the usual position beneath (or dorsal to the loop of the gut). The proximal end of the vas deferens is from the right side almost at the end of the gland, and extends in a slight loop around on to the dorsal side of the gland to extend anteriorly alongside the rectum.

LARVAE: These are present only in colonies from Point Peron in January 1948 (AM Y1335). There are mature ♂ follicles and sperm-filled vas deferens in Swain Reefs specimens of October, 1974 (QM G9930). Neither mature gonads nor larvae were present in large colonies from Heron I. in either March or December.

The larvae are large and almost spherical, 2·5 mm. The adhesive organs have unusually short stalks and the adhesive cone and surrounding ectodermal cup are unusually shallow. There is a single blastozooid unlike the larvae of *L. voeltzkowi* and *L. bistratum* which have two. There are plant cells around the posterior end of the larva outside the posterior haemocoelic chamber. There is also an unusually large number of ectodermal ampullae (about 15 pairs) with a rounded cap of modified columnar ectodermal cells on the tip of each.

REMARKS: Michaelsen (1920) interpreted the course of the vas deferens as an incipient spiral. However, unlike *Didemnum* spp. the ascending part of the vas deferens is on the opposite side of the gland to its point of origin. Its relationship to other species of the genus *Lissoclinum* rather than *Didemnum* is also unmistakable in respect of other characters. The cloacal system, the presence of blastozooids in the larvae, the modification of the branchial lobes, the virtual loss of the peribranchial cavity, the absence of a retractor muscle and the long narrow stigmata all resemble the condition observed in *L. voeltzkowi, L. bistratum* and, with the exception only of the branchial lobes, *L. punctatum.* It is distinguished from all others by the great range in the size of the spicules and by the solid thick gelatinous colony that it forms. Although the larval form has similarities with the other *Lissoclinum* spp. above, it is also distinguished by its greater size.

Didemnoides ternatanum Gottschaldt is described with a coiled vas deferens. An examination of the type in the Hamburg Zoologisches and Staats Institut Museum has shown it to be a small colony of the present species.

This is the most robust of the plant-bearing didemnids, and with *Didemnum molle*, is found at greater depths than is usual for this group of species. Despite the greater depth at which the species is found, the plant cells are further screened from light by the high gelatinous translucent ridges on the upper surface.

Lissoclinum punctatum Kott, 1977
(Figs. 24, 25; Plate 2·3)

Lissoclinum punctatum Kott, 1977, p. 620.
Lissoclinum molle: Newcomb and Pugh, 1975, p. 533.

MATERIAL EXAMINED

NEW RECORDS: Green I.: August 1979, amongst rubble near reef edge, LWM, QM G12456. Nelly Bay, Magnetic I.: August 1978, QM G11916. Heron I.: October 1979, cryptic, in pools below LWM near reef edge, QM G12624. Fiji, Viti Levu, July 1979: Vuda Pt. fringing reefs in pools outer reef flat, QM G12451 (with embryos); Malevu, fringing reefs in pools, outer reef flat, QM G12452, (with embryos); Makaluva reef, in pools, outer reef flat, QM G12462.

PREVIOUSLY RECORDED: *Lissoclinum punctatum* Kott, 1977, Holotype QM G9920; Paratypes QM G9426, G9926. *Lissoclinum molle:* Newcomb and Pugh, 1975, QM G8592.

DISTRIBUTION

RANGE: Great Barrier Reef: Lizard I., Green I., Heron I. (Kott 1977; new records). Fiji: Viti Levu (new records).

HABITAT: The species is found just below low tide, in cryptic habitats, usually on coral skeletons.

DESCRIPTION

COLONY: These are small, investing and very thin. They are bright green, with capsules of white spicules around each zooid. These are clearly seen through the test. The colonies are very soft and often disintegrate into a stream of mucus where attempts are made to scrape them from the substrate. In life, the plant cells are contained in common cloaca. However the test disintegrates so readily when the colony is disturbed that they are often found mixed with the test in the preserved material. There may be some dark spherical pigment cells in the surface test. The common cloacal cavity is large and extends posterior to the zooids but only occupies the upper half of the colony. The lower half consists of basal test. Spicules are present only in the capsules that surround the zooids, mature ova and embryos. They are spherical, 0·01–0·03 mm in diameter and are composed of radiating flat ended rods.

ZOOIDS: The zooids are small and each is completely enclosed in a capsule of spicules. The branchial aperture has 6 shallow lobes. The atrial aperture is wide exposing most of the branchial sac. There is a small, comma-shaped lateral organ from either side of the endostyle between the second and third rows of stigmata. There are about 8 long narrow stigmata in each of the 4 rows. Fine muscle fibres from the thorax extend down onto the oesophageal region but do not form a retractor muscle. The gut loop is simple and horizontal. There is a straight vas deferens that hooks around the posterior end of the single ♂ follicle at its proximal end.

LARVAE: Mature eggs and some tailed embryos are present in specimens from Malevu and Vuda Point (QM G12451 and G12452) in July 1976 and mature ova were present at Green I. in August, 1976 (G12456). Other colonies taken in May, August and September at various locations on the Great Barrier Reef did not contain mature gonads. However, the fact that these small colonies are present at all suggests that breeding may occur throughout the year. The tailed embryos are large (0·6 mm) and the tail is wound right around the larval trunk. They are not sufficiently well developed, however, to determine their structure. No blastozooids can be distinguished, although the larval thorax is very small and the developing oesophageal neck is long as in *L. voeltzkowi*, *L. bistratum* and *L. patella*, all of which do have larval blastozooids. However, the yolk mass is anterior to the developing oozooid as in other species in which there is no larval blastozooid. (In those larvae with buds the yolk mass is always posterior to the oozooid and its buds).

REMARKS: The zooid of this species is similar to others in the genus *Lissoclinum*. It is characterised by the small very soft colony and the capsule of small spherical spicules around the zooid. The 6 branchial lobes distinguish it from the three lissoclinid species discussed above in which the branchial lobes are modified.

Echinoclinum triangulum (Sluiter 1909)
(Fig. 26; Plate 2·4)

Diplosomoides triangulum Sluiter, 1909, p. 86.
Lissoclinum triangulum: Kott, 1977, p. 620.
Echinoclinum triangulum: Millar, 1975, p. 241.
Echinoclinum philippinensis Tokioka, 1967, p. 93.

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic below LWM near reef edge, QM 12623.

PREVIOUSLY RECORDED: *Lissoclinum triangulum*: Kott, 1977, QM G9466, G9793, G9932. *Echinoclinum philippinensis* Tokioka, 1967, Types USNM 11791, 11790.

DISTRIBUTION

RANGE: Indonesia: Saleyer, Amboina (Sluiter 1909, Millar 1977). Philippines (Tokioka 1967). Great Barrier Reef: Heron I. (Kott 1977).

HABITAT: The species occupies cryptic habitats in the rubble zone, and on the edge of the reef below the low water mark down to 20 m.

DESCRIPTION

COLONY: The colonies are flat, soft, and yellowish green. Most records are of colonies less than 1 cm in length. One specimen from Heron Island at 20 m (G9466) is 6 cm long and 0·5 cm thick. There are spherical brown pigment cells in the test and the body walls of the zooids in some of the larger specimens. The whole test is filled with larger bladder cells. Beneath the superficial layer of test there is (in the larger colonies) a layer of spicules that become increasingly sparse towards the base. Spicules are always more common around the zooids, and in the smaller colonies the spicules are absent from the remainder of the test and only form a sparse coat around the zooids.

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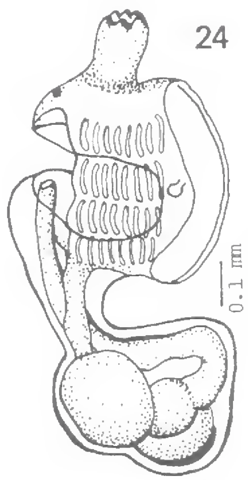

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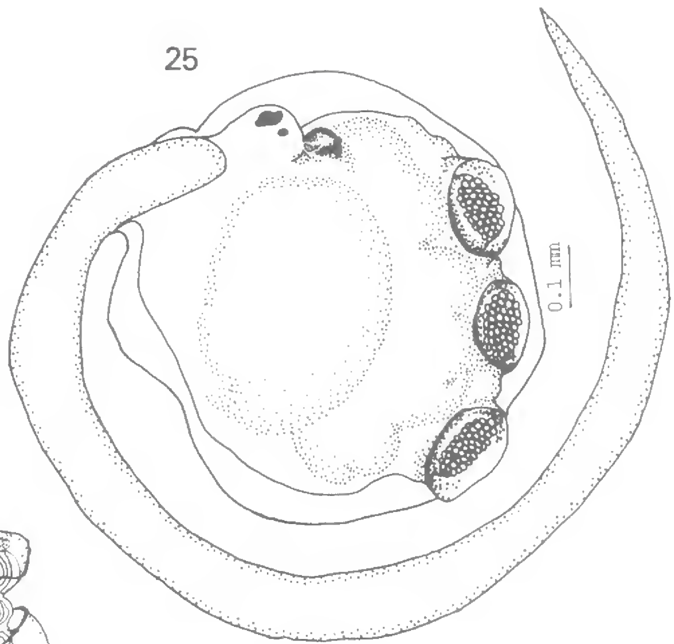

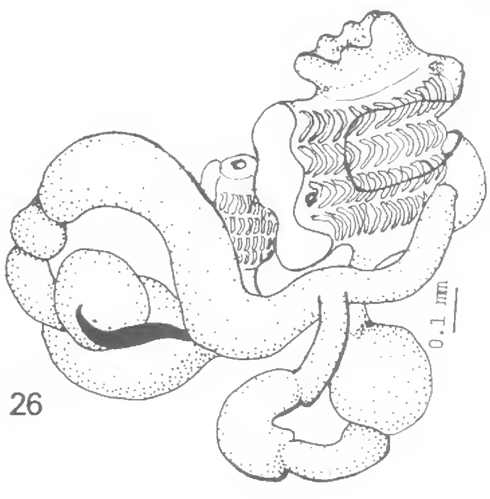

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FIGS. 24–25: *Lissoclinum punctatum* (QM 12452) — 24, zooid; 25, embryo.

FIG. 26: *Echinoclinum triangulum* (QM G9466) — zooid with blastozooids.

The spicules are made up of fine pointed rays of varying length, grouped together to form a thickened central area that gradually flattens toward the periphery, where it is drawn out into 3–6 points, sometimes resembling the outline of a small asteroid echinoderm. The spicules are 0·03 to 0·08 mm in greatest diameter (from point to point). The secondary common cloacal cavity between the zooids is thoracic. However a very extensive posterior abdominal space extends to the surface around large groups of zooids that are joined to the basal test by a single test connective crossing the posterior abdominal cavity. Plant cells are present in the test and in the common cloacal cavity.

ZOOIDS: The thorax and abdomen are each about 0·5 mm in length and the abdomen is bent up alongside the thorax. There are 6 shallow branchial lobes and a distinct sphincter muscle. The atrial aperture is wide and exposes most of the branchial sac when it is extended. There are 4 rows of 12 very delicate narrow elongate stigmata. There is a small narrow lateral organ that projects inwards on either side of the endostyle between the second and third rows of stigmata. There is no retractor muscle. The gut forms a straight simple loop. In freshly preserved material the stomach and the corresponding (glandular) part of the ascending limb of the intestine are clear yellow. The proximal part of the vas deferens extends anteriorly from the mid-dorsal surface of the single ♂ follicle. It is not hooked around the posterior border of the gland from its ventral side as is usual in *Lissoclinum*.

LARVAE: Although specimens from Heron I. taken in December have mature ♂ follicles no colonies have yet been taken from the Great Barrier Reef with mature ♀ gonads. Colonies without mature gonads have been collected in September and October at Heron I.

Millar (1975) found larvae in the base of one of the colonies he examined. They are 0·45–0·6 mm with a deep, almost spherical trunk and a short slender tail wound only about one third of the distance around the larval trunk. The adhesive organs have very slender stalks and shallow ectodermal cups. There are 6 ectodermal ampullae, two on each side of the base of the stalks of the adhesive organs and a dorsal and ventral ampulla. The cells on the tips of the ectodermal ampullae appear to be modified. The larval thorax is large and there are no blastozooids. There is an anterior yolk mass at the base of the ampullae.

REMARKS: The origin of the straight vas deferens from the mid dorsal surface, is the same as in *Echinoclinum verilli*. The present species and *E. verilli* are accordingly afforded a generic status that is distinct from the closely related *Lissoclinum*. A vas deferens of this type has also been described for *Diplosoma handi* Eldredge 1967 (see below: *D. virens*).

The present species is also distinguished by the presence of plant cells in the test, the form of the spicules, the thoracic cloacal system, and the orientation of the abdomen that is flexed up against the thorax. The larva is also different from *Lissoclinum* larvae, having no blastozooids, a deep larval trunk, deep thorax, very slender adhesive organs and stalks, an anterior yolk mass and few ectodermal ampullae. Kott (1977) mistakenly recorded 2 ♂ follicles. The testis is undivided in this species.

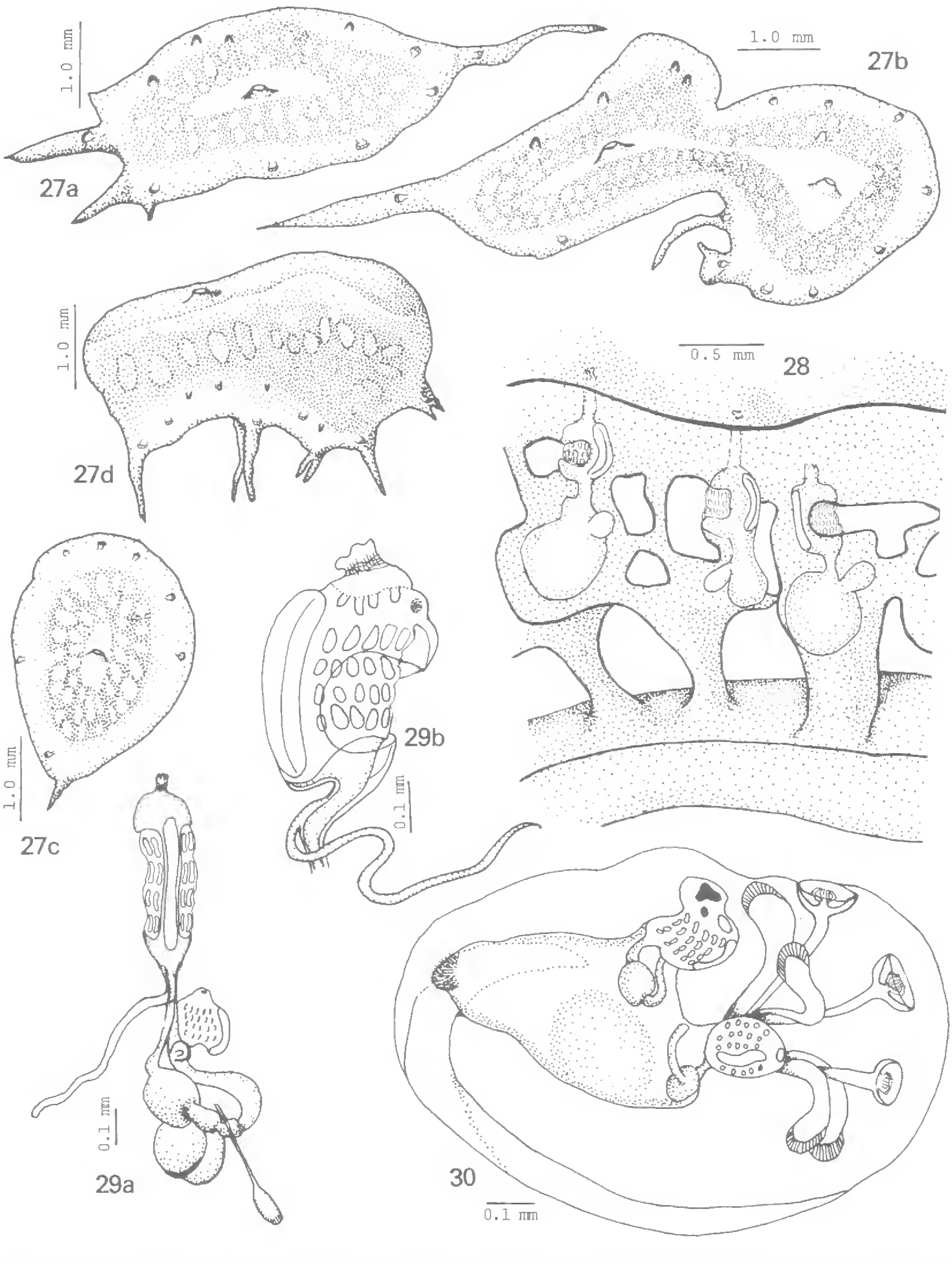
Diplosoma virens (Hartmeyer, 1909)
(Figs. 27–30)

Diplosoma viride Herdman, 1906, p. 341.
Leptoclinum virens Hartmeyer, 1909, p. 1456. Tokioka 1943, p. 500; 1967, p. 68. Kott, 1966, p. 291.
Diplosoma virens: Hastings, 1931, p. 102. Newcomb and Pugh, 1975, p. 533. Thinh and Griffiths, 1977, p. 673. Thinh, 1978, p. 617.
Leptoclinum simile Sluiter, 1909, p. 77 (part).
Leptoclinum varium Sluiter, 1909, p. 80.
Leptoclinum calificiforme Sluiter, 1909, p. 82. Van Name, 1918, p. 160
Not *Leptoclinum viride* Herdman, 1906, p. 34 (< *Didemnum viride*)
Not *Diplosoma virens:* Eldredge, 1967, p. 228. Kott, 1977, p. 620. Thorne, Newcomb and Osmond, 1977, p. 575. (< *Diplosoma similis*).

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic, below LWM near edge of reef, QM G12631. Green I.: August 1979, inner sandy reef flat on *Halimeda*, QM G12484. Fiji (Viti Levu) July 1979: Vuda Point, fringing reef, in pools, outer reef flat, QM G12486; Malevu, fringing reef, in pools behind cascades and on inner sandy reef flat, QM G12485 (some larvae); Makaluva reef, inner sandy reef flat, QM G12461.

PREVIOUSLY RECORDED: *Diplosoma viride* herdman, 1906, Holotype BM 1907.8.30.42. *Diplosoma virens:* Newcomb and Pugh, 1975, QM G8593; Kott, 1977 (Heron I.), QM G9797, G9445, G9882, G9888, G9937 (with embryos); Kott, 1966 (Darwin), AM 1119 (with larvae) *Leptoclinum varium* Sluiter, 1909, Syntypes ZMA TU.599.6, TU.599.8, ZMA TU.597. *Leptoclinum calciforme* Sluiter, 1909, Holotype ZMA TU.573. *Leptoclinum simile* Sluiter, 1909, Syntype ZMA TU.591.2 (with larvae).



FIGS. 27–30: *Diplosoma virens* (QM G1285, colonies; QM G12484, zooids; QM G9937, larva) — 27, colonies (a–c, upper surface; d, side view); 28, section through part of a colony; 29, zooid (a, with extended thorax; b, contracted thorax); 30, larva.

DISTRIBUTION

RANGE: Ceylon (Herdman 1906). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I., Low Is., Green I., Heron I. (Hastings 1931, Kott 1977). Indonesia (Sluiter 1909). Palau Is., Gilbert Is., Philippine Is., Marshall Is (Van Name 1918, Tokioka 1967). Fiji: Viti Levu (new records).

HABITAT: The greatest depth recorded for this species is from off Amboina at 40 m (ZMA TU.599.6) and there are other records from similar depths. It is also found often on the open reef flat and around the sides of pools and on weed where it is just covered with water at low tide. At Heron Island the colonies are larger than is usual for the species, and are found along the reef edge and in surge channels amongst strands of living coral down to 5 m.

DESCRIPTION

COLONY: The usual appearance of the living colonies is very adequately described by Herdman (1906, p. 341): '.... numerous small rounded colonies closely placed .... The centre of the colony where the common cloaca is placed is depressed and of a paler green colour. The zone of ascidiozooids is also paler, while the outer ring of the colony, outside the ascidiozooids is the darkest and is usually of a very rich green colour.' The living colonies are rounded egg-shaped or almost spherical. They closely resemble the sea-weed, *Caulerpa,* with which they are often associated. The depression is the centre of the upper surface that is referred to by Herdman is present only in contracted or preserved specimens. In larger specimens this depression causes the colonies to assume the 'saucer' shape described by Sluiter (1905) for *D. caliciforme.* The preserved specimens are yellowish mustard-green grey or brownish-yellow and opaque. The colonies are oval, up to 1 cm long and 2–5 mm thick. Colonies on the reef edge, in surf channels, at Heron I. are up to 2 cm long and about 5 mm thick. The common cloacal aperture, from the centre of the upper surface, is on a conical or occasionally a cylindrical protruberance. The latter may be bent over, to lie more or less flat over the surface of the colony, with the upper rim incised in a V extending back along the surface of the cylinder. The borders of the colonies are vertical and rounded. Zooids may be numerous, arranged fairly densely around the central area, but are often in a single circle around the periphery of the colony. The colonies are only loosely attached to the substrate by a small area of the lower surface, or by numerous slender test extensions from the under surface, or from around the border or by a stout, stalk-like extension of the test from the centre of the under surface. Many of the colonies are irregularly shaped and appear to be dividing. Such a growth pattern would explain the dense aggregations that are so characteristic of the species. The colonies are quite firm and the test is very tough and apparently fibrous. There is a surface layer of bladder cells. Beneath this, the fibrous test in which the zooids are embedded is perforated by a network of rather narrow interconnecting cloacal canals that open into a more extensive basal cavity that is posterior to the zooids and traversed by short basal test connectives that anchor large groups of zooids to the base of the colony. The colony is thus divided horizontally into four layers all of approximately equal thickness, viz.: the surface test, the zooid bearing layer perforated by a network of narrow canals, the posterior abdominal cloacal cavities, and the basal test. These layers are present in even the smallest colonies. The complicated network of thoracic canals, and the tough, rigid colonies cause the plant cells to remain trapped inside the preserved colonies and contribute to the opacity of the colonies. They are translucent only in the depressed central area where the cloacal cavity lies beneath the central aperture. The zooids can be removed from their tough test sheaths only with the greatest difficulty. Stolonic vessels extend from the abdominal regions of the zooids into the test connectives and especially into the basal test around the periphery of the colony.

ZOOIDS: In the preserved material the zooids are whitish with clear yellow stomach and glandular portion of the intestine. Sometimes there is some brown pigment in the abdominal body wall. Zooids are small, about 1 mm long. The thorax and abdomen are of equal length. There is active budding from the neck, with up to two sets of blastozooids present at the one time. The oesophageal neck is often very long. There are 5–6 rounded to oval or elliptical stigmata in each of the 4 rows. The stigmata are lined by rather flat epithelial cells. The atrial aperture is very wide, exposing most of the branchial sac. The branchial siphon is quite narrow with a pronounced sphincter muscle. There is a long retractor muscle that is free from about half way down the

oesophageal neck. The thoracic musculature between the rows of stigmata and extending into the retractor muscle from the dorsal and ventral borders of the zooid, is fine but conspicuous. The abdomen forms an angle with the thorax and is flexed from the base of the oesophagus. The stomach is roomy and elongate. There are two ♂ follicles dorsal to the gut loop and a single straight vas deferens swollen and proximally hooked around the posterior border between the two lobes of the gland.

LARVAE: Larvae were present in colonies from Darwin in October 1965 (Kott 1966). A few were present in colonies from Heron I. in March 1975 and from Malevu in July 1979 and from the Celebes in January 1900. They are large, the larval trunk being slightly more than 1 mm long. The tail is wound about three quarters of the way around the trunk. There are usually three large median adhesive organs (one embryo was observed to have only two). There are two thick pairs of ectodermal ampullae, with modified columnar cells around their free ends. The oozooid has a large otolith and ocellus. There is a single blastozooid. In mature larvae there is a deep division between the oozooid and blastozooid. The latter remains associated with the frontal stalk from which the ectodermal ampullae and the adhesive organs arise.

In each of the *Diplosoma* species with algal symbionts there is an identical organ for the transference of plant cells from the parent colony. The name *rastrum* is suggested for the organ. In the specimens from Darwin it has not evolved beyond the stage where it is a bilateral swelling of the posterior haemocoelic chamber above the base of the tail but in the specimens from the Celebes (ZMA TU.591.2) it reaches its full development. It first appears as bilateral outgrowths of the postero-dorsal part of the posterior haemocoelic chamber, either side of the mid line above the base of the tail. The ectoderm on these swellings is modified and produced into minute scale-like projections similar to those observed on the ectoderm covering the whole posterior haemocoelic chamber in *Didemnum molle*. As the embryo matures, the bilateral swellings become continuous across the mid line and the whole postero-dorsal aspect of the larva is constricted off from the larval trunk as a more or less cylindrical transverse arc with anteriorly curving horns at either end. A narrow median stalk from that part of the larval trunk over the base of the tail supports the organ. Its central cavity is continuous with the posterior haemocoelic chamber. The test over it is differentiated into a mass of very fine threads with terminal swellings that entangle the plant cells. As the tail is withdrawn into the posterior haemocoelic chamber, the rastrum is pulled into the larval test, which also overgrows it and its adherent plant cells as the cloacal cavity of the colony is formed. This parallels the process in *Trididemnum paracyclops* (see above).

REMARKS: The species is closely related to *Diplosoma similis* with which it has often been confused. The most conspicuous distinction is the shape, consistency, size and form of attachment of the colony, and the form of the common cloacal system. The zooids of *D. virens* are smaller and more narrow than those of *D. similis* and the stomach is shorter. *D. virens* larva has two pairs of ectodermal ampullae instead of three. The species occupy different habitats at low latitudes although at Heron I. they are often taken together.

In his description of *Leptoclinum varium* Sluiter has not mentioned the presence of plant cells, however it is possible that he mistook these for what he reports as numerous blood corpuscles. Although the branchial siphon in the present specimens is much shorter than that figured by Sluiter, this character varies with the thickness of the surface layer of test. It is also affected by the degree of contraction of this rather muscular organ. One of the syntypes of *L. simile* (Sluiter 1909) is also identical with the present species and also contains plant cells, confirming the identification. It is possible that in these specimens plant cells were mistaken for pigment cells.

The colonies of *Diplosoma handi* Eldredge, 1967 from the Caroline Is. resemble this species in their size, thickness, tough solid test, high cloacal apertures and the presence of vascular stolons in the thick basal test. They are distinguished by the absence of the posterior abdominal portion of the cloacal cavity. In this and other characters they resemble *D. similis*. The course and position of the gut loop, bent up alongside the thorax, the restricted cloacal cavity, the long branchial siphon and the vas deferens (which appears to extend anteriorly from the centre of the dorsal surface of the single ♂ follicle and is not hooked around from the other surface of the gland) are all reminiscent of *Echinoclinum triangulum*.

Diplosoma similis (Sluiter, 1909)
(Figs. 31–33)

Leptoclinum simile Sluiter, 1909, p. 77.
Diplosoma virens: Eldredge, 1967, p. 228. Millar, 1975, p. 241. Kott, 1977, p. 620 (part). Thorne, Newcomb and Osmond, 1977, p. 575.

MATERIAL EXAMINED

NEW RECORDS: Green I.: August 1979, outer reef flat on rubble, QM G12480. Fiji, Viti Levu, July 1979: Deuba, in pools, reef edge, LWM, QM G12013 (turquoise colour), QM G12014 (green colour), QM G12450 (teal blue colour); Malevu, in pools behind reef crest, QM G12454 (with larvae); Makaluva in pools behind reef crest, LWM, QM G12465; Tailevu, in crevasses near reef edge, LWM, QM G12006; Suva Barrier Reef, in pools near reef edge, LWM QM G12456; Serua in depression in sandy Reef flat, LWM, QM G12012. Line Is., Christmas I.: February 1979, on reef flat, QM G12010 (with larvae).

PREVIOUSLY RECORDED: *Diplosoma virens:* Kott 1977, QM G9924, G9789 (Lizard I.); G9923 (Townsville, Magnetic I.); G9795, G9880, G9883 (with larvae), G9884, G9885, G9886, G9889, G9933, G9934, G9935, G9936, G9938, G9939, G12634, G12635, G12636, G12637 (Heron I.). *Leptoclinum simile* Sluiter, 1909, Lectotype ZMA TU.591.1.

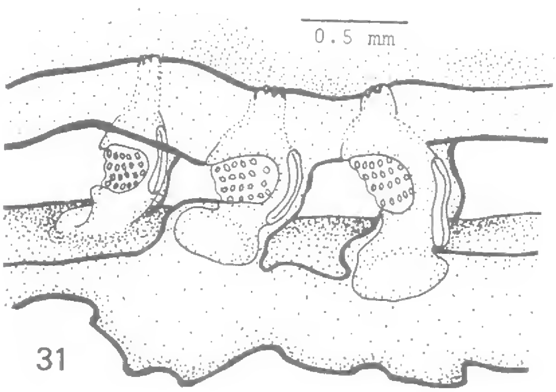
DISTRIBUTION

RANGE: Great Barrier Reef: Lizard I. to Heron Is. (Kott 1977). Indonesia (Sluiter 1909). Eniwetok, Mashall Is., Hawaii (Eldredge 1967). Line Is.: Palmyra (Eldredge 1967), Christmas I. (new records). Fiji: Viti Levu (new records). Philippines (Millar 1975). ? Japan: Tokara Is. (Tokioka 1954).

HABITAT: The species is usally found near the edge of reefs where it binds together the rubble (including coral skeletons) that collects in pools and crevices. At Heron Island it is seldom exposed directly to the light but occupies more cryptic habitats deeper down amongst the rubble. At lower latitudes, including Fiji, Low Isles and Darwin it is often found directly exposed to the light, lining the sides of pools behind the reef crest.

DESCRIPTION

COLONIES: These form thin encrusting sheets that are often very extensive. They adhere closely to the substrate by the whole of their basal surface, and their surface contours are irregular, corresponding with the contours of the substrate. They are seldom more than 2 mm thick. Their growth is not limited by the size of the substrate, for around the borders of the colony it often



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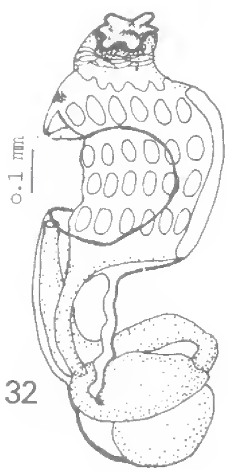

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FIGS. 31–32: *Diplosoma similis* (QM G9883) — 31, cross section through a colony; 32, zoid.

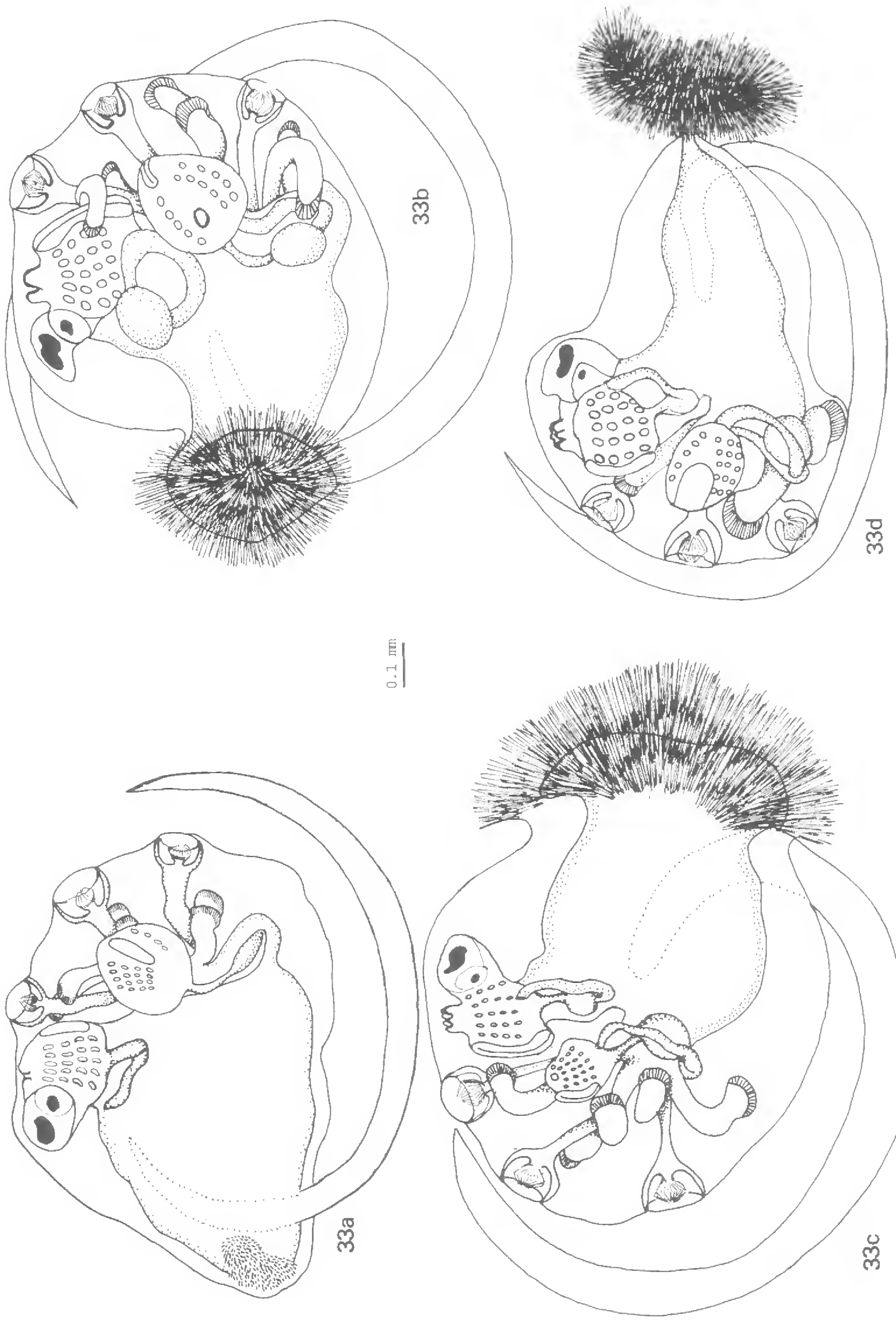


FIG. 33: *Diplosoma similis* (QM G9883) — larva showing development of rastrum (a, ectoderm cells project from postero-dorsal swelling of posterior haemocoelic chamber; b, c, rastrum is constricted off from remainder of larval trunk, hairs develop; d, arc shaped rastrum with upturned horns connected to larval trunk by a narrow neck, posterior end of larva narrows).

extends beyond the surface to which it is fixed until it attaches to an adjacent surface. Its capacity to bind rubble together results from this growth pattern that enables it to span the spaces between adjacent surfaces. The basal test is uneven and is often thickened where it fills in the irregularities in the surface to which it is attached. The colour of the living colony is very variable and may be almost any shade of dark, almost navy blue, bright green, or a whole range of teal or turquoise blue colours. The colonies at Heron I. are invariably green with patches of irridescent blue on the surface. Further to the north green colonies still occur but colonies of various shades of blue occur more often. At Low Is blue colonies of this species are the most common ascidian of the reef flat (I. Bennett, pers. comm.). In preservative the colonies become brownish green to grey as the plant cells lose their colour, and are themselves lost from the open common cloacal cavity. The test is translucent and without any other pigmentation. It is firm and gelatinous, but is not hard or tough, and is easily torn. The cloacal apertures are inconspicuous and sessile. The surface layer of test occupies about one third of the thickness of the colony, with a superficial layer of bladder cells. The anterior ends of the zooids are embedded in this surface layer. The common cloacal cavity is open, surrounding the test connectives that enclose the zooids between the surface and basal test. Zooids are not clumped together to any extent and are often suspended in the cloacal cavity by individual strands of test. Around the borders of the colony especially the common cloaca does not extend posterior to the zooids, and the abdomens are embedded on the basal test. In the centre of larger colonies, however, the cloacal cavity is more extensive and extends posterior to the zooid around the base of the long test connectives. Normally the cloacal cavity and the basal test each occupy about one third of the thickness of the colony, except where the basal test is thickened to accommodate irregularities in the substrate (see above). In some colonies there are clouds of an opaque white or brown particulate deposit in the test.

Zooids: Zooids are 1 mm long. They are very evenly spaced in the test. The gut is at right angles to the thorax and there is a moderately long oesophageal region. The branchial siphon is well developed with a conspicuous sphincter muscle and 6 triangular branchial lobes. There is a moderately long prepharyngeal region. The atrial aperture is wide exposing most of the branchial sac. There are 4 rows of 6 round to oval stigmata. There is a fairly long retractor muscle that usually extends beyond the posterior end of the body. It is free from the body from a point near the branchial sac. There are stolonic vessels with the usual terminal ampullae projecting from the abdomen into the basal test. There are up to two sets of blastozooids. The body wall over the gut loop usually contains brown pigment although this is often lost in preservative. Occasionally the whole body wall of the zooid contains brown pigment. The abdomen is usually bent at an angle to the thorax from the base of the oesophagus. The stomach is especially long and roomy and gradually narrows at the pyloric end. It occupies almost the whole of the proximal limb of the gut loop. There are two ♂ follicles and the vas deferens is straight.

Larvae: These are present in the larger colonies in July, February, December, and March and there is no indication of seasonal breeding. They are large, 0·8 mm long, excluding the posteriorly projecting rastrum or plant rake. The tail is wound three quarters of the way around the larval trunk. There is an oozooid with otolith and ocellus, and a single blastozooid. There are 3 pairs of slender ectodermal ampullae, each with modified columnar cells forming a swelling at the free end. The ectodermal ampullae branch off either side of the frontal stalk that supports the three median adhesive organs. In the mature larva, there is a deep division between the oozooid and the blastozooid. The latter remains associated with the frontal stalk. There are many larvae present in the common cloacal cavity that display a fully developed rastrum (see above, *D. virens*).

Remarks: The species is distinguished from *Diplosoma virens* principally by the form and size of the colony, the simple two dimensional common cloacal system and absence of the conspicuous protruding cloacal apertures. The colony is less solid than that of *D. virens* and the plant cells are completely lost from the common cloacal cavity much more readily. The branchial sac is larger than in *D. virens*. The dark pigment in the body wall of the zooids is also characteristic of the present species — although it has often completely disappeared in the preserved material. The stomach is long and roomy and occupies almost the whole of one limb of the gut loop. The larvae of the two species are also similar and can be distinguished only by three pairs of ectodermal ampullae in the present species and a better

developed rastrum. The synonymy of specimens previously assigned to *D. virens* with *D. similis* Sluiter, is based on the consistency, the thickness and colour of the colony and the size and form of the zooids, the gut loop and the branchial sac.

The synonymy of *D. midori* (Tokioka 1954) was suggested by Eldredge (1967). The pyloric end of the stomach is more enlarged than in the present species. The retractor muscle of *D. midori* is shorter and more delicate, and the thoracic musculature is also more delicate than in the present species.

Diplosoma midori (Tokioka, 1954)
(Figs. 34, 35)

Leptoclinum midori Tokioka, 1954, p. 11.

MATERIAL EXAMINED

NEW RECORD: Tonga: coral reef, LWM, coll. R. Lewin, 17.4.76 QM G12669

DISTRIBUTION

RANGE: Japan: Tokara Is. (Tokioka 1954). Tonga (new record).

HABITAT: The species is taken on coral reefs.

DESCRIPTION

COLONY: A single colony is available. It is an irregular sheet 4 cm in maximum extent and up to 5 mm thick. Part of the border projects as a free lamella with thick internal test and a layer of zooids on both sides and around the border. The test is gelatinous and translucent, the zooids showing as dark and whitish points. The surface layer of test is very thin indeed. The zooids are contained in test connectives that cross the cloacal cavity joining basal to surface test. The basal test is very thick. Here and there the surface test is produced into protruding common cloacal apertures. The plant cells are contained in the common cloacal cavity.

ZOOIDS: The zooids are evenly distributed. They are about 1·5 mm long. The branchial opening is almost sessile and muscles are very inconspicuous. The retractor muscle is very fine and short. There are 4 rows of 6 delicate oval stigmata. The thorax is delicate. The gut loop is relatively short and slightly flexed ventrally. The stomach is long and roomy and occupies the whole length of the proximal limb of the gut loop. There are two ♂ follicles. The abdominal body wall of the preserved specimens is darkly pigmented.

LARVAE: These are 1·6 mm long. The tail is wound only one third of the distance around the larval trunk. There is a single blastozooid and the rastrum is especially well developed in the mature embryoes. In a few specimens the proximal end of the tail is withdrawn into the haemocoelic chamber of the left rastral horn. This may be an artefact resulting from the fixation and preservation of the colony. There are the usual 3 adhesive organs and 4 pairs of long slender ectodermal ampullae with modified terminal cells.

REMARKS: The species is distinguished from *D. similis* and *D. virens* by the very thin surface test, sessile branchial aperture, very delicate thorax and short fine retractor muscle. The zooid is distinguished from that of *D. multipapillata* by its delicate collapsible stigmata and the long roomy stomach. The colony of the present specimens is also distinctive in its double sided lamellae, that project free from the colony. In this it bears some resemblance to *Diplosoma perspicum* Sluiter, 1909 (> *D. translucidum* Hartmeyer, 1919). No plant cells have been located in the latter species which is further distinguished by its long, narrow stigmata. The free lamellae have not been described for the Japanese specimens, many of which were small colonies. It is most probable that there is considerable variation in this character, however, as there is in *Diplosoma virens* (above).

The 4 pairs of ectodermal ampullae distinguish the larvae from these of all other species.

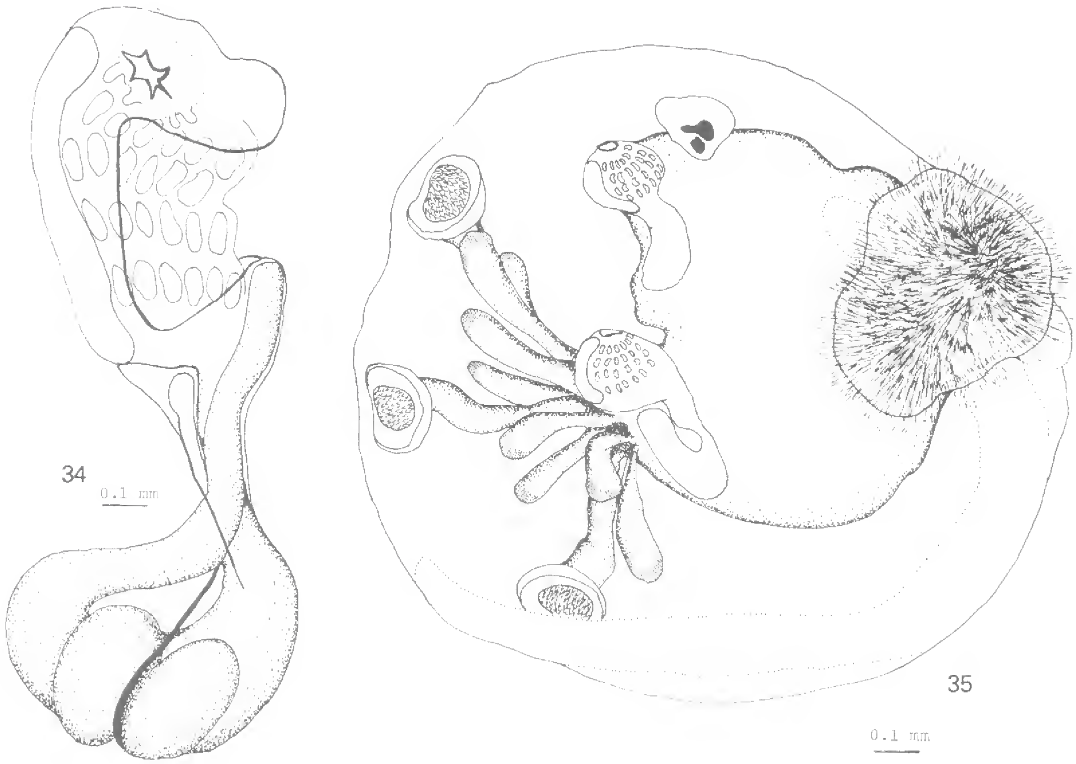
Diplosoma multipapillata n. sp.
(Figs. 36–39)

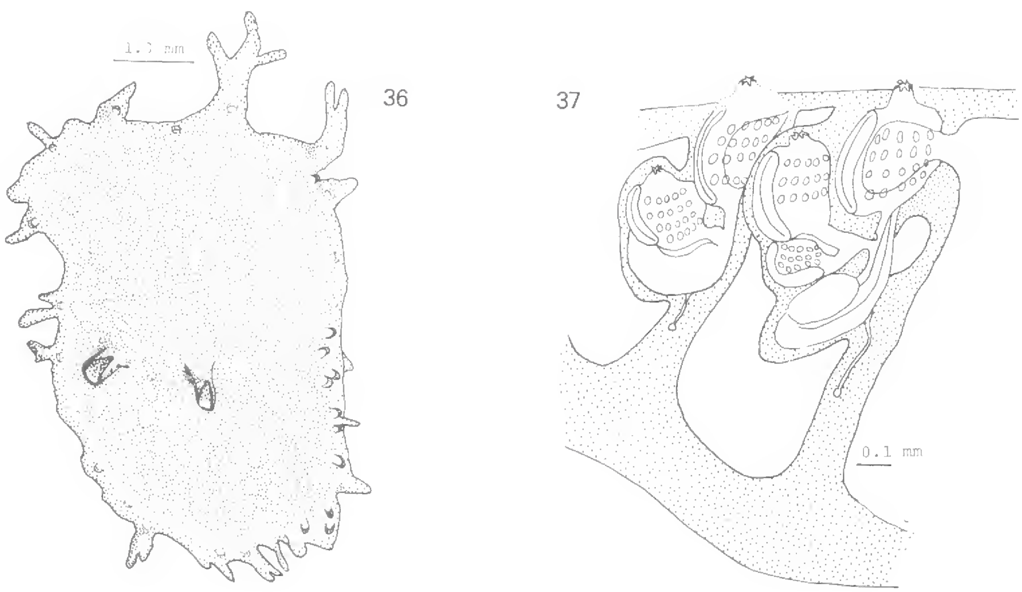
MATERIAL EXAMINED

NEW RECORDS: Malevu, Viti Levu, Fiji: fringing reef, close inshore, under cascades, coll. PK, 11.7.79. Holotype: QM G12487, Paratypes: QM G12488.

DISTRIBUTION

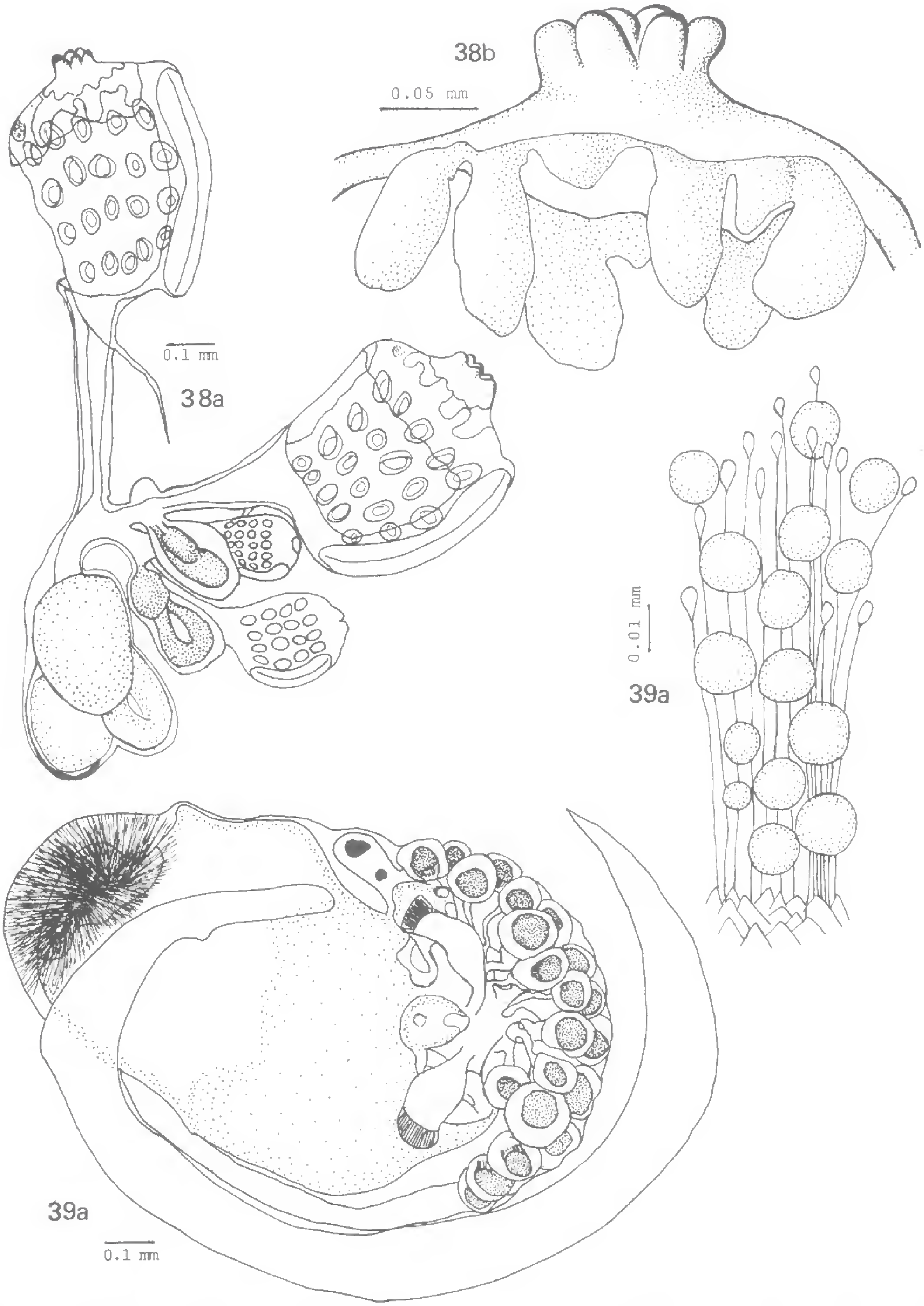
RANGE: The species has been taken only from the type location, where it is prolific and conspicuous.





FIGS. 34–35: *Diplosoma midori* (QM G12699) — 34, zooid; 35, immature larva.

FIGS. 36–37: *Diplosoma multipapillata* (QM G12487) — 34, colony, upper surface; 35, cross section through colony.



FIGS. 38–39: *Diplosoma multipapillata* (QM G12487) — 36, zooid (a, zooid with blastozooids; b, branchial aperture and tentacles); 37, larva (a, whole larva; b, rastral hairs entangling algal cells).

HABITAT: It occurs close inshore, along the secondary or riverine rim of the fringing reef where it is bissected by the river channel that extends at right angles from the shore. The small colonies lie in profusion on the surface of the algal mat that covers this riverine rim and extends for a short distance down the upper gently terraced riverine slope. Here the waters of the reef flat drain into the river channel from about mid tide when the crest is exposed. The habitat is therefore swept by fast undirectional cascades of reef flat water for about half of each tidal cycle.

There are similar cascades of reef flat water into river channels at other points along the south western fringing reefs of Viti Levu but the species apparently occurs only at Malevu.

The habitat is a stringent one, and the species appears to be isolated in it (see below, Remarks).

DESCRIPTION

COLONY: The colonies are a brilliant blue colour. In preservative this fades to a dull green, and later green-brown. Colonies are seldom more than 1 cm long, and are roughly elongate, elliptical, oval or irregular. They are about 1·5 mm in maximum thickness. The borders of the colony and parts of the basal surface are produced into branched holdfasts. The shape of some of the colonies suggests that they are lobulating. There is only a very narrow clear area around the border, the remainder of the surface being the brilliant blue of the plant cells lining the cloacal cavity. The whitish ampullae of the stolonic vessels from peripheral zooids are conspicuous in this translucent border.

The surface and the basal test are especially thin and the common cloacal cavity is very extensive, and is crossed by zooids embedded in individual test sheaths. The common cloacal apertures are on fairly long narrow cylinders that are bent to lie horizontally across the upper surface. Their upper rim is often incised in a deep V that extends back along the upper surface of the tube.

ZOOIDS: Zooids are crowded in the colony. They are about 0·8 mm long. There is no branchial siphon and the aperture is sessile, with 6 rounded lobes. There does not appear to be a sphincter muscle. The ring of 6 large and rather swollen branchial tentacles that alternate with shorter ones is just inside the aperture. The prepharyngeal area is narrow. There are 4 rows of 5 absolutely circular stigmata with relatively small openings. The cells lining the stigmata are deep and the pore is actually a short cylinder through the gut wall. The circular diameter of the pore is firmly maintained, tending also to maintain the branchial sac in a fully expanded condition. The atrial apertures are wide exposing all of the branchial sac. There are 3 and sometimes 4 sets of oesophageal blastozooids. There is a short, slender retractor muscle with very few fibres. The oesophageal neck is very long. The gut is bent at a slight angle to the thorax. Although most colonies contained larvae, there were no mature ♂ follicles and it is assumed that they were spent. There appears to be a single ♂ follicle. The vas deferens is straight, its proximal end hooked around the posterior border of gland.

LARVAE: These are large, about 1·3 mm long. The tail is wound almost all the way around the mid line of the trunk. On the right side of the anterior end of the larva there is a swelling from which 30 separate adhesive organs develop. In the mature larvae these spread out over the front. There is an oozooid with an ocellus and otolith and a single blastozooid. There are 3 pairs of long ectodermal ampullae with especially large columnar cells over the free end. The rastrum (see *D. virens,* above) develops from the postero-dorsal part of the larval trunk, just above the base of the tail as in *D. virens.* There is a deep furrow that develops in the larval ectoderm and test, around the rastral area. In due course, this is separated from the larval trunk as an inflated horizontal arc with upturned horns that lies transversely across the posterior end of the trunk supported by a narrow median stalk. The central cavity of the rastrum is in continuity with the posterior haemocoelic chamber. The rastral hairs are thick and stronger than those of *D. virens* and appear to become less tangled. They clearly differentiate from the larval test in this region, and they appear to be associated with the enlarged overlapping ectodermal cells of the rastrum. The exact details of the relationship between the ectoderm, the test and the rastral hairs will be determined through histological studies that are beyond the scope of the present work. Before metamorphosis the posterior end of the larval trunk narrows, and the rastrum, with the plant cells gathered from the parental cloacal cavity, is drawn inwards, partly by the overgrowth of the larval test, and partly by

the withdrawal of the posterior haemocoelic chamber, as the tail is drawn in, prior to its resorption.

REMARKS: The species is clearly most closely related to *D. similis* through its two dimensional cloacal cavity, well developed larval rastrum and ectodermal ampullae. The colonies superficially resemble those of *D. virens* but they are much flatter. The species is most clearly distinguished from both by its extraordinary larval adhesive apparatus. Adhesive strands of test that often form a continuous fringe around the borders of the colony are also much more conspicuous than in *D. virens*. The cylindrical cloacal apertures lying across the upper surface in the direction of the current flow are also a feature that sometimes occurs in *D. virens* but is more consistent and conspicuous in the present species. The prolific vegetative blastozooid production that is associated with proliferation of the colonies through lobulation, the sessile branchial aperture and large tentacles, the reduced musculature and very short, slender retractor, the small circular cylindrical stigmata and inflated thorax are also distinctive. The adaptive characters that distinguish this species from others are consistent with the requirements of its stringent habitat and suggest a possible explanation for its isolation and speciation.

The adaptations are those that enable the colonies to effect and maintain rapid and firm attachment to the substrate, to maintain their population density for sexual reproduction (Kott 1974) and to accommodate the fast unidirectional current that flows over them for about half of each tidal cycle (while the salinity in this inshore extent of the river channel is at its lowest). Thus, it is possible that the river provides the barrier to dispersal of those larvae that have not effected immediate fixation following their release from the parent colony. This barrier could be effective only if larvae are not released when the tide rises above the reef crest and the freshwater runoff from the river is minimal. This requirement would be satisfied if larvae are released through the narrow cloacal aperture only when a strong current flows over the surface of colony. No data are available at present to support this hypothesis. However the release of larvae on ebbing spring tides is known for many marine species (Johannes 1978) and enhances selection for free swimming larvae to maintain gene flow in tropical waters (Kott 1974). Such a stimulus to larval release, if it is present in this species, would have resulted in its isolation in the unique conditions that prevail.

CONCLUSIONS

PHYLOGENY

The characters of zooids and larvae of plant-bearing ascidians are summarised in Table 1. It will be seen that there are certain characters common to the groups of species in each genus. Species in the genus *Diplosoma* show the closest affinity with one another and differences are principally found in the larvae and colonies. It is probable that the capacity to accommodate algal symbionts occurred only once in this genus, and that speciation occurred only after the algal/ascidian relationship had been established.

Distinguishing characters between species in each of the genera *Trididemnum, Lissoclinum* and *Didemnum* do not indicate such close affinities and there is no clear indication regarding the origin of the algal symbiosis.

It is likely that a capacity for algal symbiosis was selected for separately in each of the species of *Didemnum* that demonstrate the phenomenon. *Lissoclinum voeltzkowi, L. bistratum,* and *L. patella* may represent a sister grouping having in common relatively large zooids, deeply invaginated lateral organs, larval blastozooids and similar ectodermal ampullae. *Lissoclinum punctatum* and *E. triangulum* share some adult characters with other *Lissoclinum* spp., but their larvae are different and do not suggest a relationship either with one another or with the other three species. Thus, the algal-ascidian symbiosis may have evolved on two separate occasions in *Lissoclinum* and again in *Echinoclinum*.

In *Trididemnum* the situation is confusing. The close relationships between adult zooids of *T. paracyclops* and *T. cyclops* are not supported by either the larvae or the respective methods of algal transfer. Further, although *T. clinides* differs markedly from others in the group in several respects, it does have the same mechanism of algal transfer as do *T. miniatum* and *T. cyclops*. At this stage an hypothesis that the unique method of algal transfer found in these species has been inherited from a common ancestor seems most convenient. If this hypothesis is accurate, speciation in *T. clinides, T. miniatum* and *T. cyclops* did not affect their plant transfer mechanism. In *T. paracyclops* however, isolation and speciation from *T. cyclops,* with which it shares many larval and adult characters, would have to have involved changes in the plant carrying capacity of the larvae that could be associated with its increased size. The larva of *T. strigosum* is the only one in which the plant cells are deeply embedded in the test.

Geographic Range

From Table 2, it can be seen that a range in the Indian and West Pacific Oceans is not unusual. It is also clear that records are far from complete at most locations: the majority of the widely ranging species are recorded from both the Great Barrier Reef and Fiji. It is likely that further surveys will show that a more comprehensive catalogue of species will be present over a great part of this region and that an extended range will be demonstrated for some of the species that appear at present to be relatively restricted. Habitats for some of the more common species are summarized in Table 3.

Latitudinal effects on habitat are especially evident for species that occupy exposed reef flat locations at low latitudes. *Lissoclinum voeltzkowi, Trididemnum cyclops, T. miniatum, Diplosoma virens* and *D. similis* all occur at Heron I. in cryptic habitats below low water mark near the edge of the reef. Here light values are considerably less than those they would encounter in the exposed habitats they usually occupy. It is possible that in this southern extent of their geographic range a greater diurnal temperature range on the reef flat may preclude their normal occurrence. *L. voeltzkowi,* however, only occurs occasionally at Heron I. and its range may be

TABLE 1. Summary of Characters of Algal-bearing Didemnids of the Indo-west Pacific*

	ZOOIDS										COLONY		
	Branchial lobes**	Atrial aperture	Retractor muscle	Gut loop	♂ follicles	Vas deferens spirals	Size (mm)	Endostylar pigment cap	Lateral organ	Stigmata	Number of systems/ colony***	Spicules (u): spherical (sp), Stellate (st), flattened (fl)	Plant cells:*
Didemnum													
molle	6	wide	long	long	1	6½	1·5	—	shallow	8 long	1	5–15 sp	CC
viride	6	wide	medium	long	?	?	0·7	—	shallow	5 oval	>1	30–40 st	E
Trididemnum													
clinides	6	*siphon*	*short*	medium	1	6½	1·0	none	shallow	5 long	1	30–40 st	*E*
miniatum	6	transverse	medium	medium	1	5½	*0·8*	none	shallow	7 oval	1	*10–20 sp*	*E*
strigosum	6	transverse	long	medium	1	6½	*0·5*	none	projects	7 oval	>1	*50–80 st*	*E*
nubilum	6	transverse	medium	medium	1	5½	*0·6*	none	projects	5 oval	>1	*30–50 sp*	*E*
cyclops	6	transverse	long	medium	1	5½	1·5	*present*	shallow	7 long	1	40–60 st	CC
paracyclops	6	transverse	medium	medium	1	*9½*	1·5	*present*	shallow	7 long	>1	30–80 st	CC
Lissoclinum													
voeltzkowi	*2*	wide	*none*	*short*	1	—	0·8	—	*deep*	8 medium	1	20–40 st	CC
bistratum	*2*	wide	*reduced*	*short*	1	—	0·9	—	*deep*	8 long	>1	30–50 sp	CC
patellum	*2*	wide	*none*	*short*	1	—	3·0	—	*deep*	14 long	>1	10–80 sp	CC
punctatum	6	wide	*none*	*short*	1	—	1·0	—	*deep*	8 long	>1	10–30 sp	CC
Echinoclinum													
triangulum	6	wide	*none*	*medium*	1	—	1·4	—	*deep*	12 long	>1	*30–80 fl*	*E*
Diplosoma													
virens	6	wide	long	long	*2*	—	1·0	—	none	5 oval	1	—	CC
similis	6	wide	long	long	*2*	—	1·0	—	none	6 oval	>1	—	CC
midori	6	wide	*short*	medium	*2*	—	1·5	—	none	6 oval	1	—	CC
multipapillata	6	wide	*short*	long	*1*	—	0·8	—	none	5 *round*	1	—	CC
handi	6	wide	*short*	long	*1*	—	1·0	—	none	6 oval	1	—	CC

* Those characters that may be considered diagnostic of a species or of groups of species appear in italics.

** A branchial siphon is present, except in *D. multipapillata* and *D. midori* where the aperture is sessile.

*** Colonies that form extensive sheets have >1 system; those with single systems may lobulate and divide to maintain the characteristically small sized colonies.

restricted by lower light levels at higher latitudes. Records show that of all the reef flat species, *L. voeltzkowi, L. bistratum* and *T. cyclops* have the greatest range in both oceans. Of these, *L. voeltzkowi* which normally occurs in the most exposed locations on the reef flat is most restricted latitudinally.

L. bistratum has the greatest latitudinal range of the reef flat species, its southern limit being off south eastern Queensland and its northern limits at the Tokara Is and the Red Sea. *Diplosoma virens* and *D. similis* have a similar recorded east-west range in both oceans. Although neither is known to extend west of Sri Lanka at present, *D. similis* is the only plant-bearing species known from Hawaii. The reef slope species *D. molle* and *L. patellum* also occur in both oceans. They are both common at Heron I. and are also known from Cockburn Sound. The former is also recorded from Okinawa and its latitudinal range is as extensive as that of *L. bistratum*. *Didemnum viride* (Ceylon and Madagascar) and *Trididemnum paracyclops* (Great Barrier Reef) have more resctircted ranges and only *Trididemnum strigosum* and *T. nubilum* (Philippines), *Diplosoma multipapillata* (Fiji), and *D. handi* (Caroline Is.) are endemic.

TABLE I (cont.)

	LARVAE								
	Ectodermal cups	Adhesive organs	Ectodermal ampullae	Modified ectodermal cells on ampullae	Blastozooids	Yolk mass††	Plant cell transfer	Size (mm)	Distribution†††
Didemnum									
molle	*deep*	3	2 prs	none	*2*	posterior	posterior barrel	0·9	IWP
viride	?	?	?	?	?	?	?	?	WI
Trididemnum									
clinides	medium	3	3 prs	none	none	anterior	*trunk encased*	0·6	WP
miniatum	medium	3	3 prs	none	none	anterior	*trunk encased*	0·7	WP
strigosum	medium	3	6–8 prs	none	none	anterior	*embedded*	*1·1*	E(P)
nubilum	?	?	?	?	?	?	?	?	E(P)
cyclops	medium	*2*	2 prs	none	none	anterior	*trunk encased*	0·5	IWP
paracyclops	medium	*2*	*4½ prs*	none	none	anterior	*posterior cap*	1·0	GBR
Lissoclinum									
voeltzkowi	medium	3·2	8 prs	*present*	*2*	posterior	posterior cap	1·5	IWP
bistratum	medium	3	8 prs	*present*	*2*	posterior	posterior cap	1·0	IWP
patellum	*shallow*	3	*15 prs*	*present*	1	posterior	posterior cap	*2·5*	WP
punctatum	medium	3	(?6 prs)	?	(?none)	*anterior*	?	0·6	WP
Echinoclinum									
triangulum	medium	3	3 prs	(?present)	*none*	*anterior*	?	0·6	WP
Diplosoma									
virens	medium	3	*2 prs*	present	1	posterior	rastrum	1·0	IWP
similis	medium	3	3 prs	present	1	posterior	rastrum	1·0	WP
midori	medium	3	*4 prs*	present	1	posterior	rastrum	1·5	WP
multipapillata	*shallow*	*30*	3 prs	present	1	posterior	rastrum	1·3	E(F)
handi	?	?	?	?	?	?	?	?	E(C)

† E=embedded, cc=in cloacal cavity.

†† The position of the yolk mass is apparently related to the presence or absence of blastozooids.

††† IWP — Indo-west Pacific; WP — West Pacific; GBR — Great Barrier Reef; E (P,C,F) — Endemic (Philippines, Caroline Is, Fiji); WI — West Indian Ocean

TABLE 2: GEOGRAPHIC RANGE OF PLANT-BEARING DIDEMNID ASCIDIANS.*

Species	Zanzibar 5°S	Malagasy 20°S	Red Sea 20°N	Sri Lanka 8°N	Indonesia 10°S	Darwin 10°S	Cockburn Sd 32°S	GBR 10 to 24°S	Mooloolaba 28°S	Borneo 0°	Philippines 10°N	Tokara Is 30°N	Okinawa 26°N	Palau Is 10°N	Eniwetok 10°N	Marshall Is 10°N	Hawaii 20°N	Gilbert Is 0°	Line Is 0°	Fiji 20°S	Tonga 23°S
D. viride		X		X																	
D. molle	X	X			X	X	X	X			X		X	X							
T. cyclops		X				X		X			X				X			X		X	
L. voeltzkowi		X						X												X	
L. bistratum			X		X	X		X	X			X		X						X	X
D. virens				X	X	X		X			X					X		X		X	
D. similis					X			X			X				X	X	X		X	X	
T. clinides								X			X				X					X	
L. punctatum								X												X	
D. midori												X									X
L. patellum					X		X	X		X				X							
L. triangulum					X			X			X										
T. miniatum								X			X										
T. paracyclops								X													

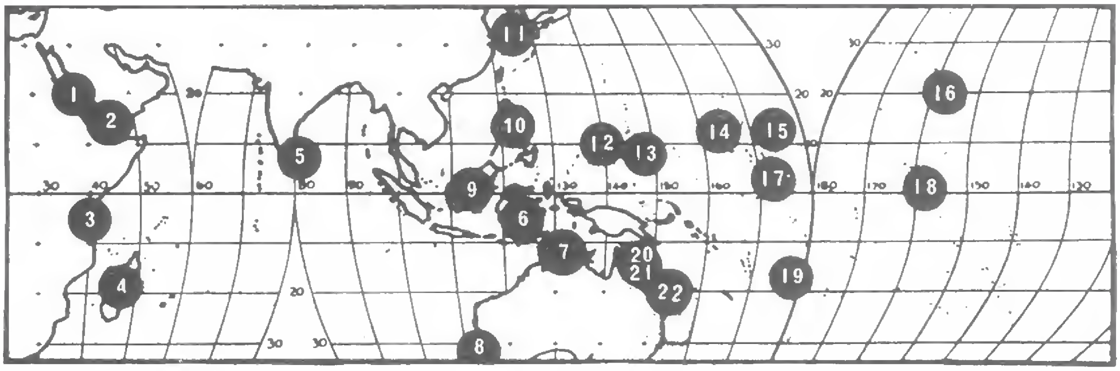
* Endemic species recorded from single geographic Locations only are not included.

The mechanism whereby these ubiquitous species avoid isolation and speciation is not known. Kott (1974) suggested that pelagic larvae are the means by which gene flow is maintained, despite opposite pressures to avoid dispersal. Crisp (1977) and Johannes (1978) have also discussed the role of the pelagic larvae of marine organisms. Where habitats are transient the role of the larvae to disperse and colonise is acknowledged. Yet it is in the tropics where habitats are not transient that sessile organisms with the free swimming larvae are most common. Johannes (1978) has explored an hypothesis that fish gametes and larvae are dispersed as a result of selective pressures imposed by predators in the parental shallow water habitats, and he has argued that some progeny are likely to be recruited back into the parent population by means of gyres or other circulatory patterns.

Crisp (1977) pointed out that dispersal *per se* is wasteful; and that adaptive advantages associated with it must therefore transcend opposite pressures to maintain populations. It is most unlikely that pressures to avoid wastage (through predators) would have caused the evolution of other strategies (such as those described by Johannes) that also promote dispersal and loss from the adult population.

TABLE 3: CHARACTERISTIC HABITATS OF REEF FLAT SPECIES AT LOW LATITUDES.

Inner sandy reef flat	Outer sandy reef flat	Living coral zone, outer reef flat (with pools)	Rubble zone and Reef rim with surge channels, pools	Reef Slope
T. miniatum *D. virens*	*L. voeltzkowi*	*L. bistratum* *T. cyclops*	*D. similis* *L. punctatum* *T. clinides*	*L. triangulum* *L. patellum* *D. molle*



1. Red Sea
2. Gulf of Tadjourah
3. Zanzibar
4. Malagasy
5. Ceylon
6. Indonesia
7. Darwin
8. Cockburn Sound
9. Borneo
10. Philippines
11. Tokara Is.
12. Palau Is.
13. Caroline Is.
14. Eniwetok
15. Marshall Is.
16. Hawaii
17. Gilbert Is.
18. Line Is.
19. Fiji
20. Lizard I.
21. Green I.
22. Heron I.

FIG. 40: Locations between Latitude 30°S and 30°N, and Longitude 30°E and 130°W where didemnids with prokaryotic symbionts have been recorded (see Table 2).

Therefore it seems likely that some advantage other than population maintenance must be associated with the existence of free swimming larvae. The length of larval life of the present species is not known. The condition of the developing adult organs and larval adhesive organs before their release from the parent colony do not suggest a long larval life. Further, the larvae are generally large and it is unlikely that their relatively short tails are especially effective swimming organs. The larvae do not appear to be ideal as vehicles for gene flow between very isolated populations (see also Crisp *loc. cit.*). Nevertheless, they appear to be the only vehicle by which gene flow can occur. Their recruitment through the chains of islands and reefs that exist around the Indo-west Pacific coralline region would explain the lack of endemism that is characteristic of this region. If they have been selected for in order to fulfil this role, it is probable that there are associated strategies that will ensure their maximum dispersal. The probability of larval release on ebbing tides when there is maximum water flow over the parent colonies is discussed above (see *Diplosoma multipapillata*, Remarks).

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Carlisle (1961) has observed metamorphosed colonies of *Diplosoma listerianum* either in mid water or attached to the surface film. Distribution of these species may therefore occur irrespective of the length of larval life.

I am also grateful to Lucille Crevola-Gillespie who drew the text figures, and to Robert Raven and Alan Easton for the Scanning Electron Micrographs. Janet Byrne typed the manuscript.

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PLATE 1

1: *Didemnum molle*, spherical spicules with loose flat ended rays, 0·005–0·015 mm (scale 0·005 mm).

2: *Didemnum viride*, stellate spicules with few long pointed rays, 0·03–0·04 mm (scale 0·1 mm).

3a, b: *Lissoclinum voeltzkowi*, spicules stellate or spherical (with blunt ended rays), 0·02–0·04 mm (scale 0·05, 0·005 mm).

4: *Lissoclinum voeltzkowi*, living colonies (Green I.).

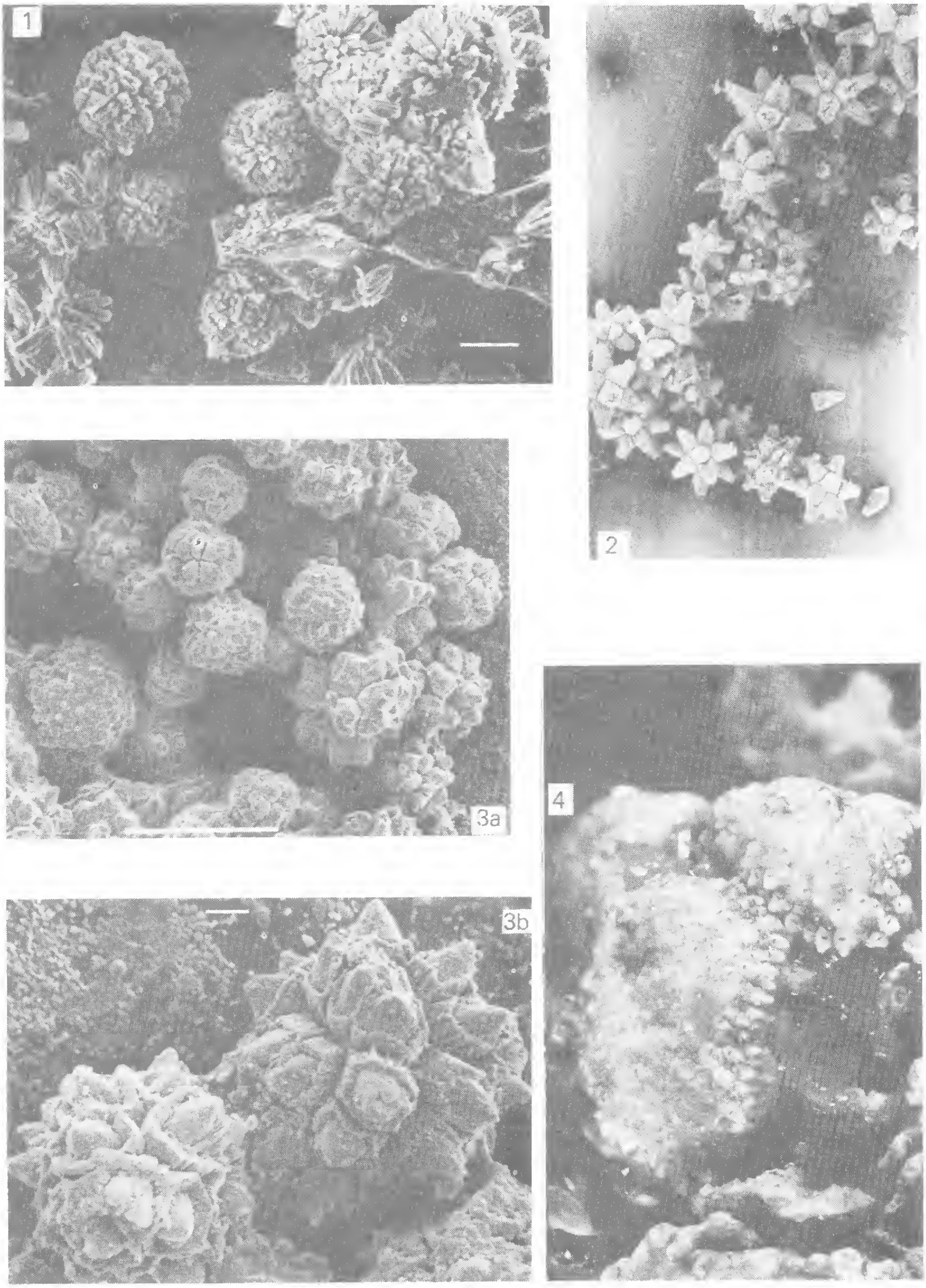
1
2
3a
3b
4

PLATE 2

1a, b: *Lissoclinum bistratum*, spicules spherical with tight blunt ended rays, 0·03–0·05 mm (scale 0·012 mm).

2: *Lissoclinum patellum*, spicules spherical with tight needle-like rays 0·01–0·08 mm (scale 0·005 mm).

3: *Lissoclinum punctatum*, spicules spherical, with slightly irregular needle-like rays, 0·01–0·03 mm (scale 0·005 mm).

4: *Echinoclinum triangulum*, spicules flat, triangular, square or trapezoid with loose needle-like rays of varying length, 0·03 to 0·08 mm (scale 0·005 mm).

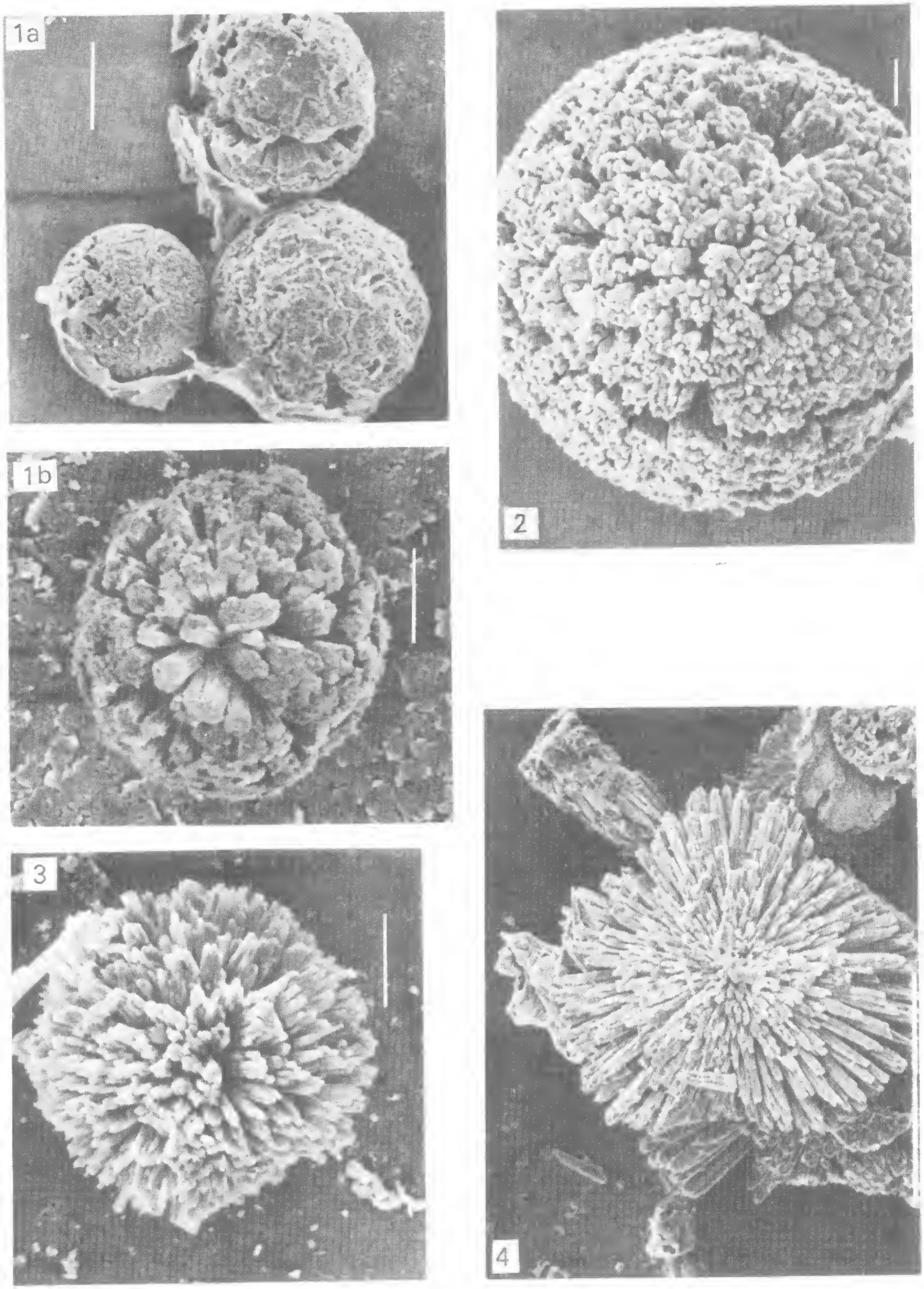
1a
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PLATE 3

1a, b: *Trididemnum clinides*, stellate spicules with rounded or conical rays, 0·03–0·04 mm (scale 0·005 mm).

2: *Trididemnum miniatum*, spherical spicules with loose flat ended rays, 0·01–0·02 mm (scale 0·005 mm).

3: *Trididemnum strigosum*, stellate spicules with few conspicuously projecting rays, 0·05–0·08 mm (scale 0·005 mm).

4: *Trididemnum nubilum*, stellate spicules with numerous short conical rays projecting, 0·03–0·05 (scale 0·01 mm).

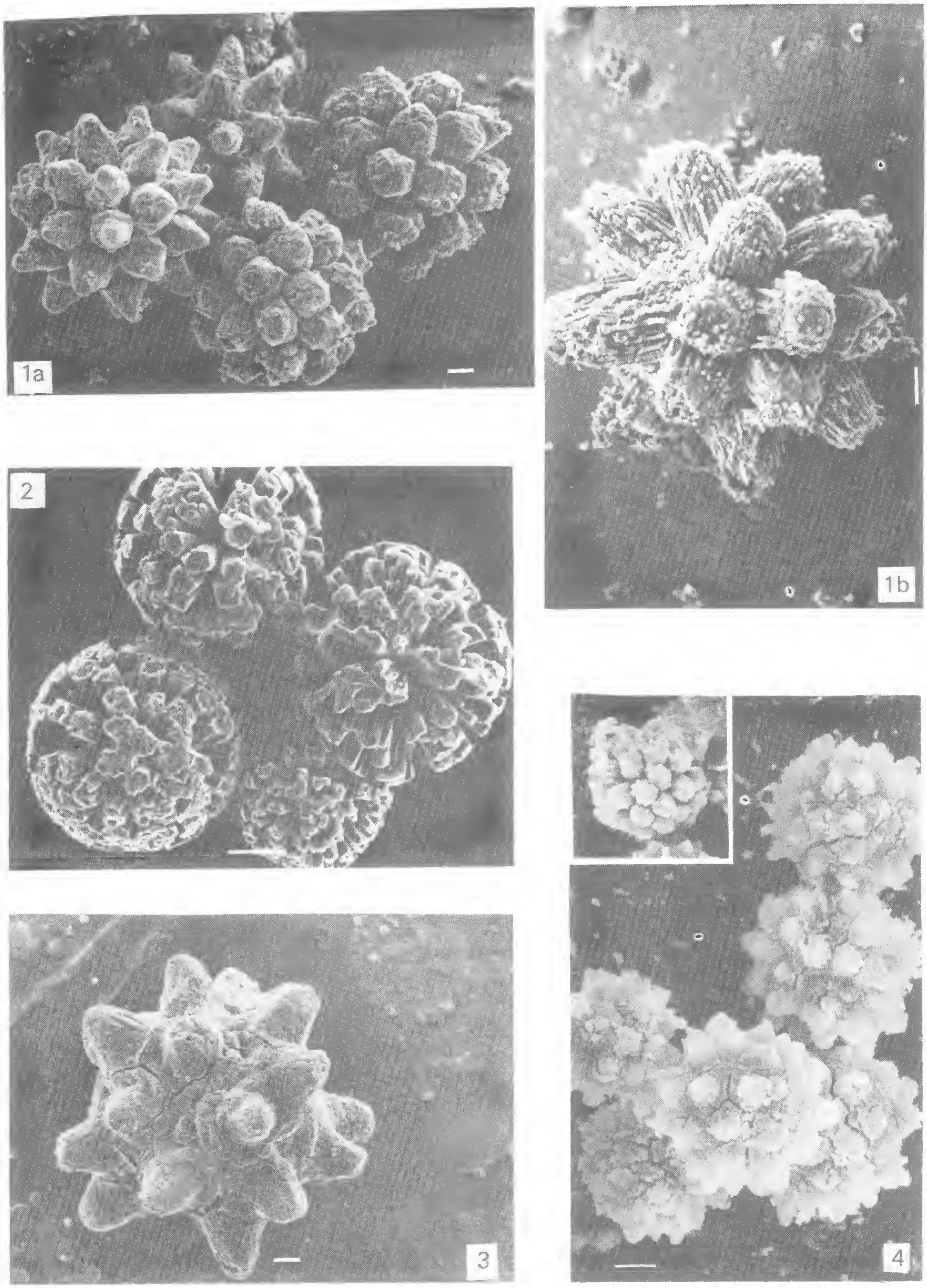
1a
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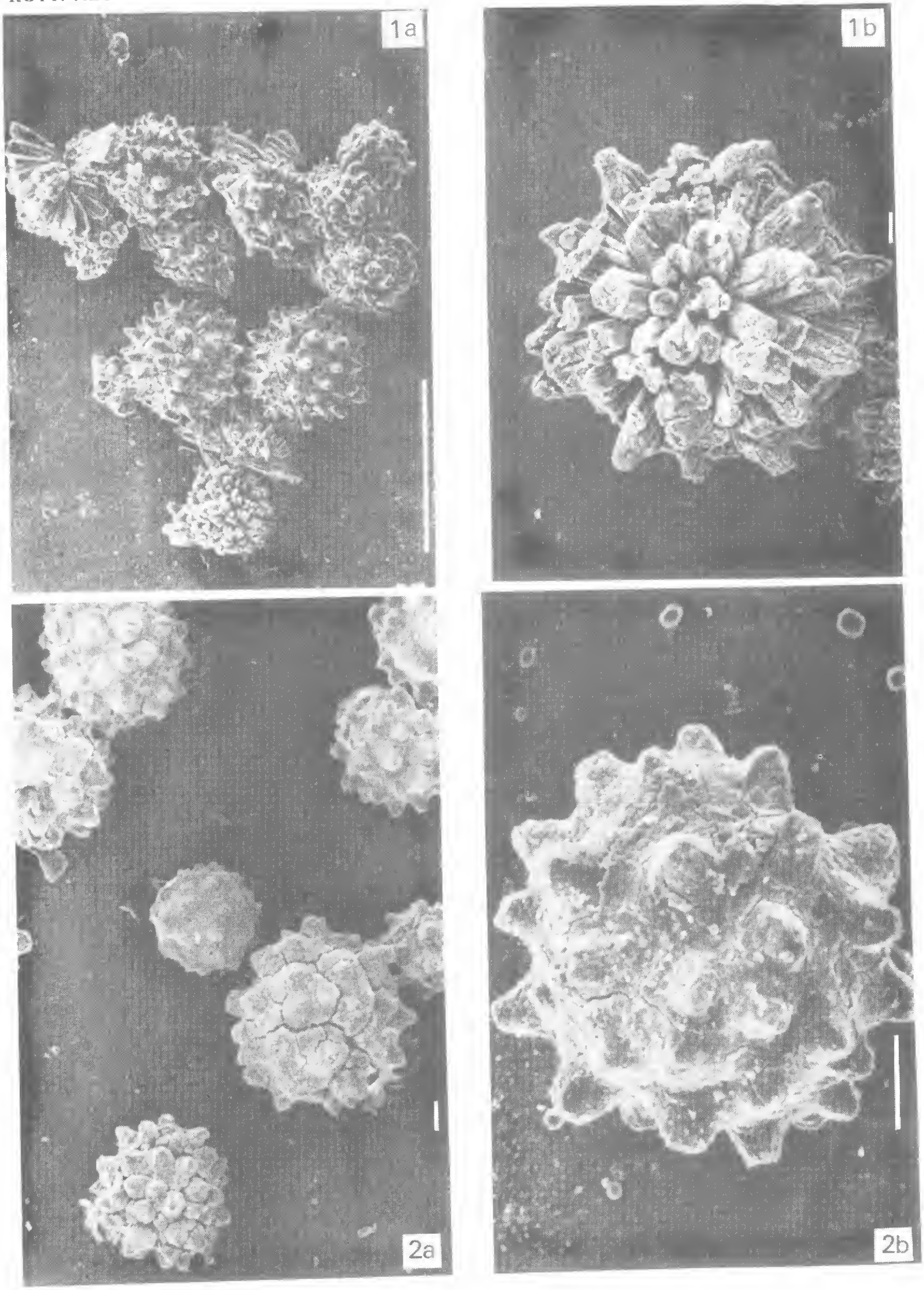
PLATE 4

1a, b: *Trididemnum cyclops*, stellate spicules with conical or flat ended rays, 0·04–0·06 mm (scales 0·05 mm, 0·005 mm).

2a, b: *Trididemnum paracyclops*, almost spherical spicules with projecting conical rays, 0·03–0·08 mm (scale 0·011 mm).



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A NEW FAMILY OF ENSIFEROUS ORTHOPTERA FROM THE COASTAL SANDS OF SOUTHEAST QUEENSLAND

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ABSTRACT

A new family, Cooloolidae, of Orthoptera is proposed, based on a single new genus and species *Cooloola propator* Rentz, from southeast Queensland, Australia. The cricket-like insect, referred to as the Cooloola monster, is an aberrant member of the suborder Ensifera. It is unusual in possessing very short antennae which, in turn, have a reduced number of articles, 10 in number. Nearly all species in all families of Ensifera have antennae with 30 or more articles. The structure of the mouthparts is unique in the Orthoptera in that the lacinia of the maxilla is larger and more developed than the mandibles. The lacinia is knife-shaped and not hooked. This suggests a piercing rather than the usual sorting and cleaning function for that structure. The mandible is elongate, indicative of a predaceous habit as opposed to short, stout mandibles which are possessed by plant feeders. *C. propator* has no close relatives but superficially resembles several species of the stenopelmatid *Oryctopus*. This genus is known from south India and Ceylon. Both genera share modification for a burrowing habit as illustrated by shortened antennae and legs, excavate, trowel-like modified spines, pale coloration, reduced eyes, and brachypterous males and apterous or micropterous females. The tarsal claw of both genera is sexually dimorphic. In females it is greatly reduced but normal in males. This may indicate a more sedentary role for females. Detailed examination of mouthparts, alimentary tract, and wing venation reveal that *Oryctopus* possesses all of the characteristic structures of the Stenopelmatidae, whereas *Cooloola* does not. The convergence of characters is interpreted as adaptation to a fossorial existence.

Cooloola propator lives in sandy, moist soils and is not particularly associated with a single vegetation type. In rainforest and open forest, the soil is densely laced with roots. There is little accumulated litter on the surface and the soil is devoid of humus. The sand is usually bare and moist. Wandering adult males have been collected at night and their above-ground activity seems to be associated with wet weather. They appear to be active after periods of rain. Females are apparently completely subterranean.

Every taxonomist is at first sceptical, and, hopefully, subsequently convinced of the reality of a new family of organisms. In an insect order such as the Orthoptera (grasshoppers, crickets, and allies), such an occurrence is extremely rare. This order is conservatively structured at the family level, despite recent escapades of several authors into the field of taxonomic escalation (see Kevan, 1977, for review). The last time a family was proposed based on an entirely new taxon was when E.M. Walker (1914) described the Grylloblattidae as a new family of Orthoptera.

This paper describes a new family of cricket-like insects, the only known representative of which is known popularly as the 'Cooloola monster'. The history of the discovery is traced, and various structures are compared with those in other Orthoptera.

The new family Cooloolidae is placed in the superfamily Gryllacridoidea based on its similarities with *Oryctopus* of the Stenopelmatidae. Although *Cooloola* Rentz gen. nov. is highly specialized in many characters, it can be assigned to the Gryllacridoidea on the basis of its tarsal formula and structure, lack of tegminal stridulatory structure, and general appearance.

History of the Discovery of the Cooloola Monster

Shortly after arriving at my new post as Curator of Orthoptera, CSIRO, Canberra in 1977 I was presented with a small parcel from Mr E.C. Dahms, Curator of Insects, Queensland Museum, Brisbane with a note 'Here's something to introduce you to the Australian fauna'. After some amusement at the technical excellence of the

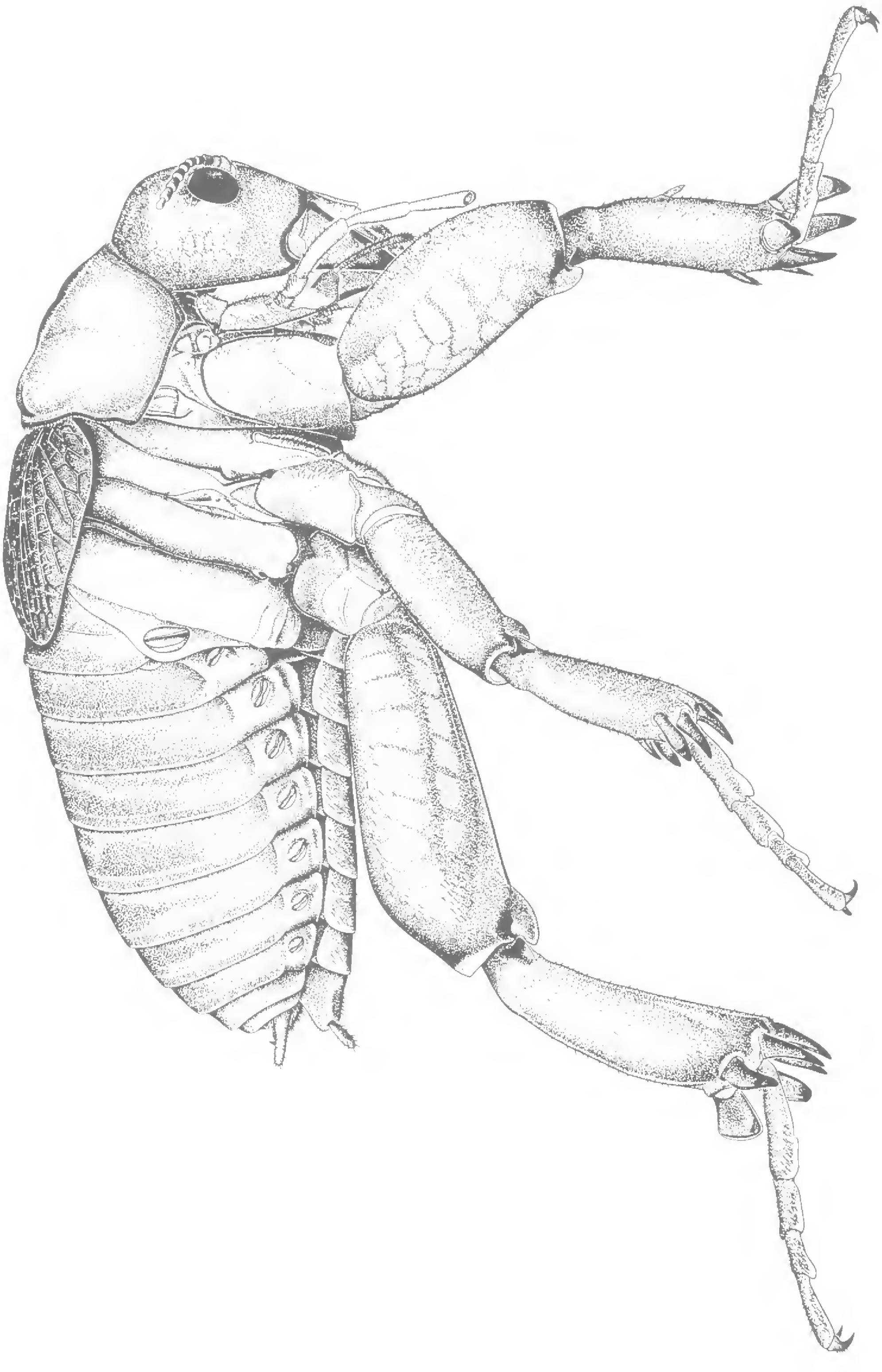

FIG. 1: Adult male of *Cooloola propator*.

apparently manufactured monster, it was determined that it was a genuine complete cricket-like insect.

The specimen had been taken by Dr V. Davies, Curator of Arachnids, Queensland Museum, in a pitfall trap set in mid-February 1976, in the rainforest of Cooloola National Park, near Gympie, Queensland. It was an adult male. A field trip to the area was planned and in the company of my wife, Mr E.C. Dahms, Mr I.D. Galloway and Dr G.B. Monteith, nearly two weeks were spent searching for the insect, but to no avail. All sorts of techniques, including digging, night searching, pitfall trapping and the oatmeal trail were used but no further specimens were located.

Subsequently a popular article concerning the interesting discovery was prepared for the news media. The article received wide circulation and had a photograph of the insect, dubbed the 'Cooloola monster'.

The second specimen, a small nymph, was collected on nearby Fraser Island by Mr T. Bade, a ranger from the National Park, on 1 July 1978. He recognised the insect from details given in the article in 'The Courier-Mail', and rushed the live specimen to the Queensland Museum, from where it was forwarded to me in Canberra.

Another trip was planned, at a different time of the year and including a few days on Fraser Island. The field work involved extensive digging and sieving soil, but the monumental efforts of those involved yielded no specimens.

Shortly after conclusion of the trip, another specimen, a live adult male, was brought into the Queensland Museum by Mr R. Nicholas. He had been camping at Freshwater Lake camping area, Cooloola National Park, and the insect crawled into his tent at dusk after a rainstorm. He recognised it as the one featured in 'The Courier-Mail' some 4 months previously.

The absence of females from the small samples was contrary to my experience with similar-looking Jerusalem crickets of the western United States. Adult males of these crickets are always difficult to obtain, and females and juveniles make up the bulk of collections (see Tinkham and Rentz, 1969, for discussion). The discovery of the fourth specimen, a female, possibly last instar nymph, ended conjecture. Its large, physogastric abdomen and short legs and tarsi indicate that the female is an obligate burrower and probably seldom walks on the surface of the ground. The specimen was found by Park Ranger Mr M. Johnston who dug it from a depth of 45 cm; the site was within 50 metres of where Mr R. Nicholas found his specimen.

The fifth specimen, an adult male was collected by Ms K. Plowman in a pitfall trap in the vicinity of Lake Cooloola. The trap had been in the ground from mid October to mid November, 1978 when it was checked.

Mr Paul Nicholas was preparing camp one evening in Aug. 1979 1 km south of Freshwater Lake in the vicinity where his father had previously found a male in Oct. 1978, and discovered a struggling cricket killed by the wheel of his automobile. It had been apparently brought to the surface by the wheels of the vehicle.

The seventh specimen was found by Mr R. Perry, who was camping near Rainbow Gorge, Fraser Island in Oct. 1979. He found it while digging a shallow hole just above the beachline.

Gutter traps based on 3 m lengths of roof guttering set in the ground so as to drain into buried buckets of formalin were designed by Dr G.B. Monteith and the author and constructed by CSIRO Division of Entomology. These were installed at the Freshwater Lake camping ground on February 4, 1979. They were checked in early May, 1979, without success, but when they were terminated on January 28, 1980, one was found to contain 5 adult males of the new insect. It is significant that a full year's trapping of insects moving on the ground surface yielded neither females nor juveniles.

Mr E. Zillman, of Gin Gin, Queensland, who was formerly with the National Park service on Fraser Island, submitted photographs of an adult female he had found on Fraser Island in June 1978. The specimen was uncovered at a depth of 22 cm around the roots of a brush box tree (*Tristania* sp.). He has seen the Cooloola monster on more than one occasion but was not aware of its importance until recently. He found one female under *Banksia* logs in sandy soil at a depth of 30 cm in a compost heap "some years before'. He is also convinced he dug one at Walla Lagoon, near Bundaberg, Queensland at 38 cm in 1952. Mr Zillman notes that his specimens were all found in sandy, and shaded soil, rich in surface roots. He considers the monster 'fairly common'.

Ecology

Although ecological information is based on only 12 specimens, we can draw a number of conclusions regarding its habits and habitat preferences. The living specimens were observed to have a radically different gait from what one expects of a cricket-like insect. The actions of the

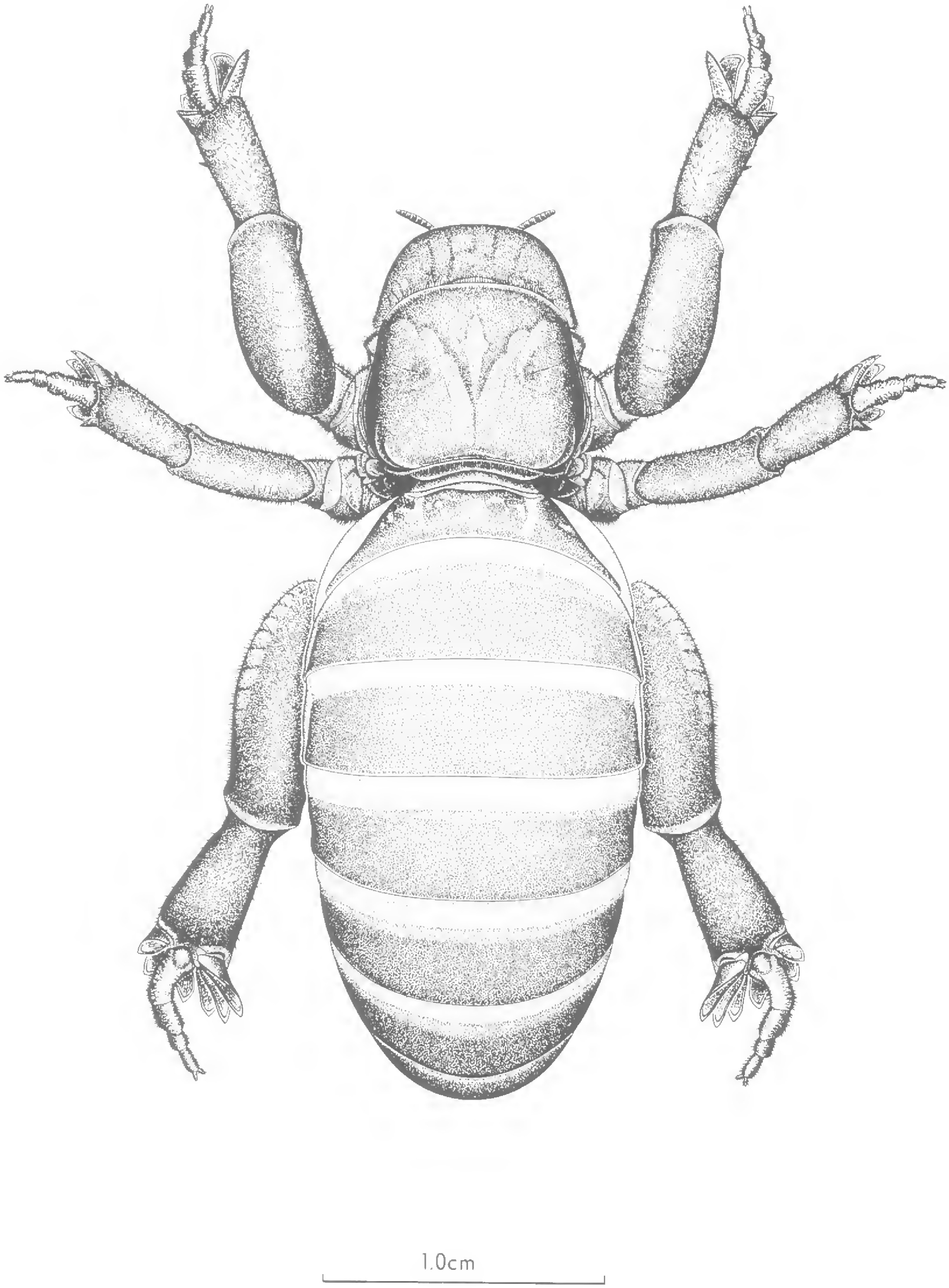

FIG. 2: Female of *C. propator*, subadult, see text.

monsters have been described as 'stomping' or tractor-like. The monster's movements are those of a fossorial creature out of its habitat. Males apparently venture forth, perhaps during rainy periods, in search of females. Otherwise they are subterranean. All specimens to date have been found within 45 cm of the surface, none deeper, although considerable digging to 3 m has been done. Mr Zillman's notes indicate the species may be associated with buried rotting wood.

Southern coastal Queensland from Coolangatta (just south of Brisbane) to Bundaberg and adjacent sandy islands, has been the subject of intensive continuous investigation by CSIRO Division of Soils and others. The area includes rainforests, sand dunes, and coastal heath habitats. It is well known locally because of the coloured 'rainbow sands'. A list of the twelve classes of landforms in the area was presented by Thompson (1975).

Watson and Arthington (1978) noted the restricted distribution of two dragonflies to acid dune lakes on Fraser Island and several other islands to the south. Ingram and Corben (1975) reported on four species of 'acid frogs' which breed only in water of low pH in wallum area of southeastern Queensland. These areas are within the range of the Cooloola monster. The wallum areas have apparently acted as islands during dry interpluvial periods. The discovery of *Cooloola propator* n. sp. in this rather limited but unique area is another indication that the habitat is peculiar and deserves protection.

The first Cooloola monster was collected from near Poona Lake, a habitat which corresponds to Thompson's Class 5, high transgressive dunes. This type of dune formation with elevations from 100-200 m is found at Cooloola, Fraser Island, and Moreton Island to the south. The dunes are formed from windblown sands from the adjacent beach. The high transgressive dunes support open forest and rainforest. The rainforest is restricted to bottoms and slopes of closed corridors, that is, dry valley bottoms. The other 11 specimens were found in Thompson's Class 4, yellow-brown transgressive dunes. These range from 30 to 60 m above sea level and have been formed from sands blown off the beaches relatively recently. This zone is relatively rich in minerals and supports moderately dense vegetation. The Cooloola monster has been found in both rainforest and open forest with 11 of the 12 specimens coming from the latter. On Fraser Island it has not yet been found in rainforest.

In areas where the insect has been found, the soil, to a considerable depth, is interlaced with tree roots. The sandy substrate is moist and there is little in the way of accumulated litter or humus on the surface. Large earthworms were not uncommon and their burrows extend to considerable depths. Other organisms were seldom encountered.

Family COOLOOLIDAE, new family

TYPE GENUS: **Cooloola,** new genus (Feminine gender)

CHARACTERISATION: The family Cooloolidae is unique among the families of Orthoptera in the following combination of characters.

Antennae reduced in length and number of articles.

Mandibles reduced in size relative to maxillae; in structure designed for grasping or tearing, not chewing; lacinia lanceolate, without hooks, designed for piercing.

Foregut extraordinarily long, extending nearly to apex of abdomen; proventriculus not hightly modified, similar to the Haglidae.

Pro-, meso-, and metapleura dorso-ventrally expanded, presenting a highly 'muscular' appearance.

Legs highly modified, femoral shape and spination of tibiae sexually dimorphic, fore femur greatly expanded dorso-ventrally, in length subequal to hind femur (more nearly equal in female); fore and hind legs (excluding tarsi) of nearly equal length; middle legs less modified, more slender.

Tarsi very elongate, sexually dimorphic; in males very elongate, in females proportionately shorter; male tarsi weakly dorso-ventrally flattened, less so in female; male tarsal claws normal, in female reduced, minute, laterally compressed; all tarsi 4-segmeted.

Tegmina present only on males, females apterous; tegmen highly sclerotized, convex, its caudal apex moulded around metathorax; tegmina separated dorsally, appearing to be capable of movement (perhaps used in burrowing); wing represented as minute, sclerotized bud.

Abdomen not highly modified in male, exceedingly bulbous in female; male cercus not suited for grasping, paraprocts platyform, each with dorsal hook; subgenital plate bearing styli. Neither sex with any kind of stridulatory apparatus.

Ovipositor short, 6-valved, not extending much beyond apex of abdomen; female subgenital plate very short, with digitiform caudal projection lying between ovipositor valves.

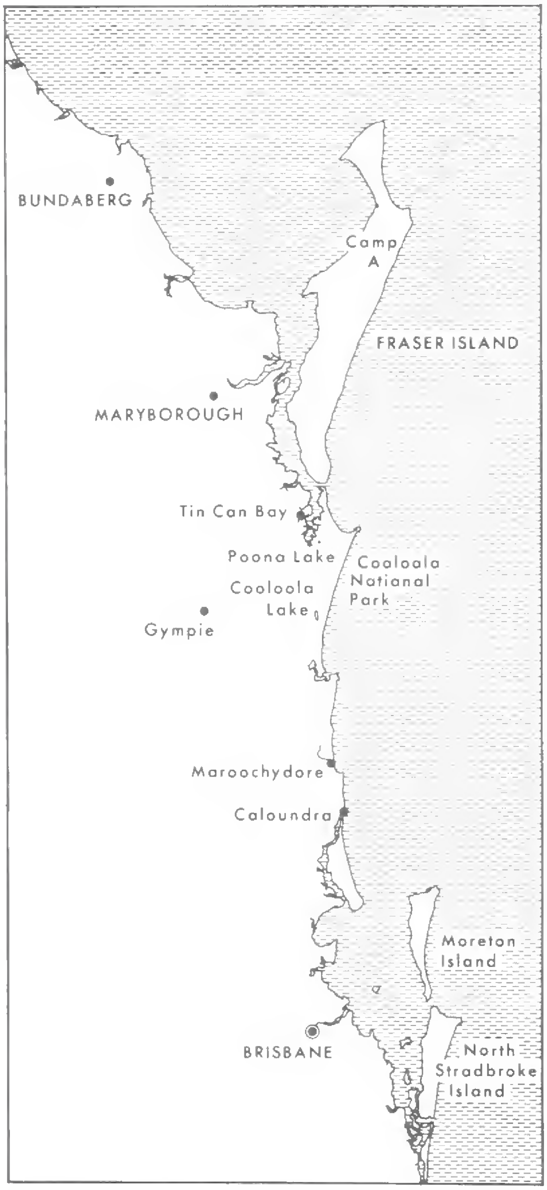

FIG. 3: Map of area inhabited by *C. propator*. See text for discussion.

Cooloola Rentz, new genus

TYPE SPECIES: *Cooloola propator* Rentz, new species, by monotypy.

DESCRIPTION

Head large, not seated in pronotum, cordate in frontal outline. Eye situated high on head, rather shallow, prominent (male) or considerably reduced (female). Labrum longer than broad; mandible obscured by lacinia, only its base visible anteriorly; maxillary palpus elongate, 5-segmented. Antenna short, with 10 articles. Pronotum broader than long, caudal margin not produced not hoodlike, only covering base of tegmen; cephalic and caudal margins both truncate to weakly obtuse, lateral lobes shallow, ventral margin straight; surface of disk relatively smooth, with two oblique lateral impressions, indicated mostly by colour. Prosternum armed with a pair of quadriform plates, divided mesad, then preceded by a pair of lateral sclerites, in turn, preceded by two pairs of linearly arranged setaceous unsclerotized lobiform processes, the more caudal pair more developed and more setaceous; mesosternum with a similar pair of plate-like processes, somewhat larger; metasternum with massive plate-like processes, caudal internal angles acutely produced. Fore coxa enormously enlarged, commencing ventrad of lateral pronotal lobe; middle coxa about half size of fore coxa; hind coxa massive. Fore and middle trochanters small, elongate; hind trochanter larger, quadrate. Fore femur short, laterally flattened, dorso-ventrally expanded, and more emphasized in female. Fore tibia only slightly longer than femur, feebly laterally compressed, not dorso-ventrally flattened; ventral surface with a single spine positioned in the middle, subapically between the two internal spurs; apex with 2 spurs on anterior margin; the more dorsal of which is short, blunt, excavate, ventral spur more aciculate, positioned ventrad of metatarsus; posterior margin with a single, subapical spine and with a pair of much longer spurs, the more dorsad of which is expanded on its dorsal surface, the more ventral more aciculate, its apex directed mesad; dorsal surface unarmed except for minute, short, stout spine positioned on external margin, this spine highly variable in size even on the same individual. Middle tibia unarmed dorsally, elongate, slender in male, short, stout, dorso-ventrally flattened in female; ventral surface with a single aciculate subapical spine positioned ventral to metatarsus;

apex bearing 6 spurs; 3 on anterior and 3 on posterior margin. Hind tibia unarmed dorsally and ventrally; apex with 6 spurs, sexually dimorphic; (male) with 3 on internal, 3 on external margin, most dorsal of internal spurs the largest, spatulate, its internal surface minutely striate, remaining spurs smaller in size, more elongate; (female) all spurs short, broad, apically excavate, surfaces striate, dorso-internal spur, in outline, ovoid, remaining spurs short, stout. Tarsi (male) tarsi elongate, claw well developed; (female) tarsi short. Prothoracic auditory structure absent; metathorax and 6 abdominal segments with well-defined spiracles. Internal surface of hind femur and adjacent portion of abdomen without stridulatory pegs. Dorsal surface of abdomen without median carina. Male terminalia: tenth tergite with a pair of small widely separated hooks; supra-anal plate simple; cercus tubular, apex blunt, not serving a grasping function; paraprocts developed, with apical hook. Subgenital plate bearing styli; no sclerotized concealed genitalia. Female terminalia: similar to male except tenth tergite without hooks, cercus somewhat shorter, more robust, subgenital plate short, supra-anal plate unmodified. Ovipositor short, scarcely projecting beyond abdominal apex, 6-valved. External margins of pronotum, legs, sterum and external ventral margins of abdomen setaceous.

Cooloola propator*, new species
(Figs. 1–14)

MATERIAL EXAMINED

HOLOTYPE: MALE (pinned), Queensland, Cooloola National Park, Rainbow Beach, near Poona Lake, February 1976, V. Davies collector, In pitfall trap, QM T8309.

DESCRIPTION

HOLOTYPE: Internal surface of hind femur and adjacent portion of abdomen without stridulatory pegs; tenth tergite basically unmodified, median portion weakly concave, lateral portions feebly produced; supra-anal plate triangular, minute; paraprocts projecting somewhat from abdomen, not appearing highly mobile; subgenital plate quadrate, fairly short; median portion without incision.

FEMALE: Differs from male in following characters: size larger, form much more robust. Fore, middle, and hind tibiae proportionately stouter, more depressed, thickened; fore tibia rugulose dorsally on external margin at apex; middle tibia very short, 1·5 times as long as greatest width. All tibial spines more robust, shorter, more blunt, trowel-shaped. Cercus tubular, apically blunt; supra-anal plate triangular. Ovipositor with dorsal valves aciculate, apex highly sclerotized, extending slightly beyond abdomen; internal valves short, stout, obtuse; ventral valves short, broadly triangular, completely concealing internal valves. Colouration: General colour tawny butterscotch brown; nymphs and female pale whitish, with following darker areas; eyes black except dorso-internal angles whitish; tegmen dark brown, veins somewhat darker; dorsal surface of pronotum with irregular brownish patches; outer pagina of hind femur with faint whitish herringbone pattern; apices of all spines and spurs dark brown or blackish; ventral surface of entire insect pale, thoracic portions darker. Nymphs and female (subadult?) almost white except for eyes and spines.

PARATYPES: 1♂, Queensland, Cooloola National Park, 7 km NE of Lake Cooloola, mid-Oct. – mid-Nov. 1978, K. Plowman, in pitfall trap QM T8310. 1♂, Freshwater Lake, 25 Oct. 1978, R. Nicholas, ANIC collection, Canberra. 1♀, Freshwater Lake camping area, 30 Oct. 1978, M.R. Johnston, QM T8311. 1 nymph, 25° 10'S 153°17'E, 19 km SSW of Indian Head, Fraser Island, National Park headquarters, Camp A July 1978, T. Bade, QM T8312. 1♀, 1 km S of Freshwater Lake Camping area, 4 Aug. 1979, P. Nicholas, QM T8313. 1♂, 1·6 km N of Rainbow Gorge, Fraser Island, 5 Oct. 1979, R. Perry, QM T8319. 5♂♂, Freshwater Camp Ground, Cooloola Nat. Park SE. Qld., 4.v.1979 – 29.i.1980, G.B. Monteith, ex guttertrap, open forest, 2 in QM (T8389 & T8390) and 3 in ANIC.

RELATIONSHIPS

The peculiar combination of characters exhibited by *C. propator* makes it difficult to determine its relationships. The presently accepted conservative classification of the Orthoptera (see Key, 1970, for example) recognizes two suborders. This division is based primarily on the number of antennal segments, 30 or more = Ensifera, i.e. katydids and crickets; 30 or fewer = Caelifera, i.e. grasshoppers, pygmy mole crickets, cylindrachetids. Were *C. propator* to have antennae with more than 30 articles, it would unquestionably be placed in the Ensifera. Its habitus is not unlike that of several of the families included therein. And the structure of the ovipositor, also of critical importance, seems within the range found in the Ensifera. I am considering the Cooloolidae as very aberrant ensiferans in the Gryllacridoidea.

*Denoting first of a kind.

TABLE 1: MEASUREMENTS (IN MM), MAXIMUM DIMENSIONS OF EACH APPENDAGE

	holotype	paratype (male)	paratype (male)	paratype (female)
Length body	23.2*	29.0	27.0	30.0
Head: depth	8.7	9.3	8.1	11.5
width	6.5	7.0	7.0	7.8
Length fore leg:				
femur	8.1	7.3	8.1	7.5
tibia	7.5	7.6	7.0	6.5
tarsus	8.8	7.2	X	4.0
Length middle leg:				
femur	6.5	7.3	6.5	7.0
tibia	6.0	5.8	5.4	4.7
tarsus	8.7	7.4	7.5	5.1
Length hind leg:				
femur	11.0	11.3	10.5	10.0
tibia	9.0	8.2	8.0	7.0
tarsus	9.8	9.8	9.0	6.8
Pronotum:				
length	5.2	6.2	5.5	6.5
width	7.5	7.7	7.7	7.1
Length lateral lobe	4.4	4.7	4.2	6.4
Length tegmen	6.4	7.1	5.3	—

*Length of body of holotype reduced because specimen is pinned, and abdomen shrunken. All others in alcohol.

Table 2 presents characters of evolutionary importance in the more closely related ensiferan families (the Grylloidea are excluded since they possess 3-segmented tarsi and a 4-valved ovipositor. These primary characters are not borne by any of the examples in Table 2. Similarly, the Tettigoniidae are excluded because most members possess a tegminal file-scraper apparatus and tibial auditory apparatus, characters, in combination, not shared by any of the listed families). The data in Table 2 indicate that there is little similarity between the Cooloolidae and either the Gryllacrididae or the Rhaphidophoridae.

I have had the opportunity to study the male type of the type species of *Oryctopus, O. bolivari* Brunner (Paris Museum) and the types of the following species of the genus: *O. prodigiosus* Bolivar, *O. bouvieri* Karny, and *O. lagenipes* Karny all in the collection of the Paris Museum. An additional subadult female apparently taken with the type of *O. prodigiosus* was sent to me from the Vienna Museum. The above species were described from the Madras area of southern India. An additional species, *O. sordellii* Griffini, not seen by me, is known from Ceylon. Not all of these species are generically related. For example, *O. lagenipes* was described without locality data. It is a late instar nymph of some other genus, perhaps the American *Stenopelmatus*. It was reported to have single-segmented antennae, but the type clearly shows this is the result of breakage. Additionally, *O. lagenipes* has mandibles typical of most stenopelmatids. The species is definitely misplaced in *Oryctopus*. The female of *O. prodigiosus* was reported to be antenna-less, but my examination of the subadult female indicates that they have been broken at the bases.

With the exception of *O. lagenipes*. the above-mentioned *Oryctopus* species show remarkable similarity in a number of characters to *Cooloola propator*. Both genera are adapted for burrowing. The legs are shortened and muscular, the spines are excavate, but in *Oryctopus* they are sharply pointed. Both genera are very pale in colour. Adult males are brachypterous or micropterous, females are apterous. The antennae are reduced in length and segment number, and although some of the types of *Oryctopus* have broken antennae, those that are entire are clearly reduced in size and segment number. The eyes of both genera are reduced, and in both this is sexually dimorphic with females showing greater reduction in the number of eye facets and in overall size of the eye. The tarsal claw of both genera is greatly reduced in females but is normal in males. On external appearance the two genera are remarkably similar (compare Bolivar's 1899 figs. 21, 21a, 21b, and Karny 1932, figs. 25, 26 with those presented here).

Detailed closer examination reveals a wide dissimilarity between the two genera. The tarsi of *Oryctopus* species are typically stenopelmatid. They are distinctly laterally compressed and the metatarsus is very elongate, longer than the remaining tarsal articles combined. In *Cooloola* the tarsi are depressed and not laterally compressed. The metatarsus is short. The mouthparts of the two genera are extremely different. As normal in the Orthoptera, the mandibles of *Oryctopus* are larger and more prominent than the lacinia of the maxilla. The reverse is true in *Cooloola*. In the latter, the mandible is not lanceolate (see Fig. 10), whereas in *O. prodigiosus* the mandible is lanceolate, without any dentition, very similar in shape to the lacinia. This cutting type of mandible in

Oryctopus appears unique in the Orthoptera. At the base of the lacinia in *Oryctopus*, several stout bristles occur; these are absent in *Cooloola*.

The tremendous expansion of the thoracic region reflected in *Cooloola* (Fig. 1) has not occurred in *Oryctopus*. In this respect, *Oryctopus* is similar to such burrowing genera as *Stenopelmatus* where the base of the legs is inserted just under the lower margin of the lateral lobe of the pronotum. In *Cooloola* (Fig. 1), the thoracic region has expanded dorso-ventrally greatly separating the base of the legs from the ventral margin of the lateral lobe of the pronotum. The sternal plates described for *C. propator* are wholly absent from *Oryctopus*. The male terminalia are quite dissimilar. In the male of *O. prodigiosus* before me, the subgenital plate is reduced, its apex acute and without styli. The cerci are erect and conical and apically digitiform.

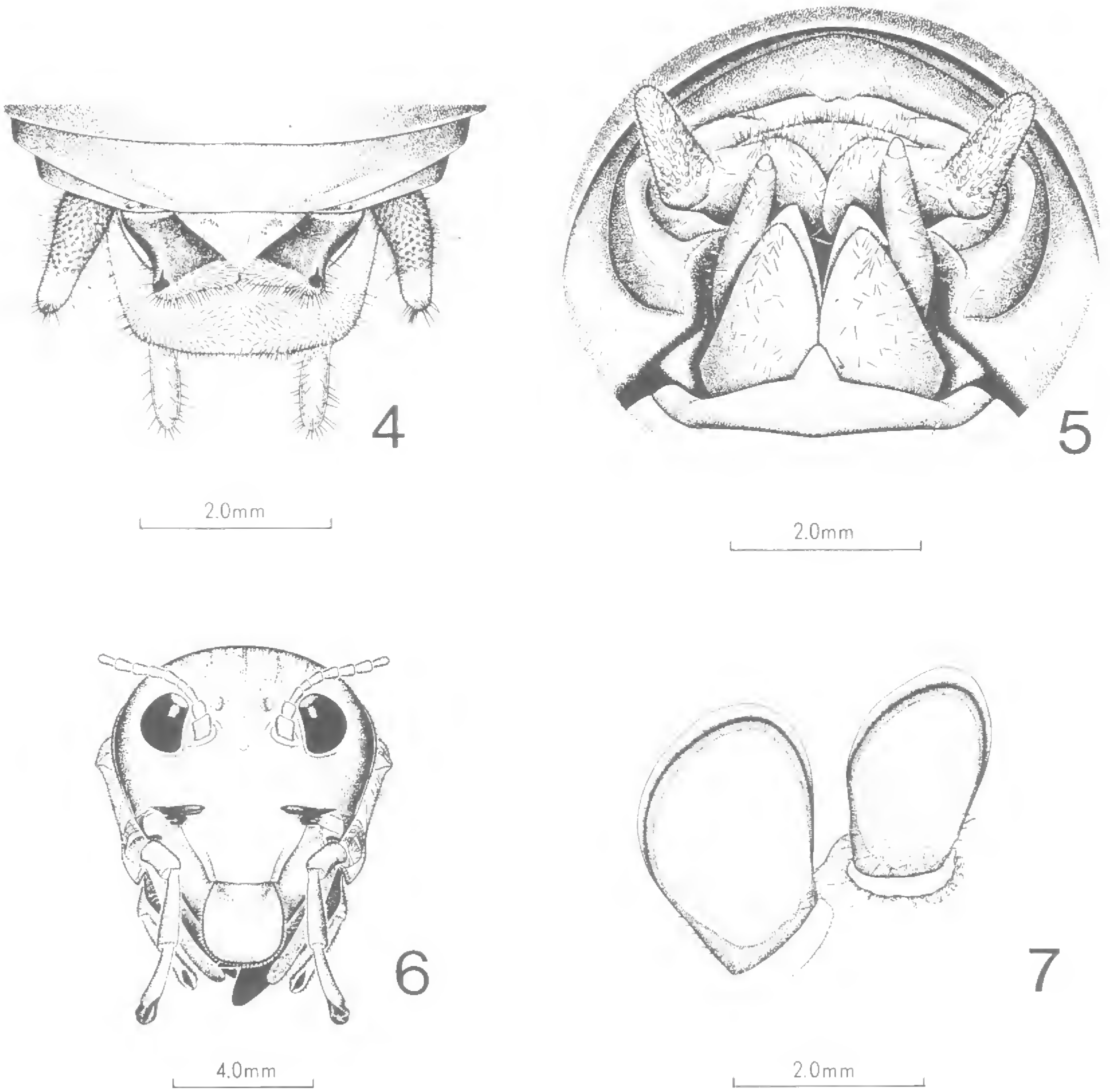

FIG. 4–7: Diagnostic structures in *C. propator*. 4, dorsal view, male terminalia; 5, caudal view, female terminalia; 6, frontal view, head of paratypic male: note protruding lacinia; 7, internal view, apical spurs left tibia, female: note striations.

TABLE 2: CHARACTERS THOUGHT TO BE OF EVOLUTIONARY IMPORTANCE IN SEVERAL ENSIFERAN FAMILIES.

CHARACTER	GRYLLACRIDIDAE	RHAPHIDOPHORIDAE	STENOPELMATIDAE	COOLOOLIDAE
Antennal sockets	widely separated	nearly touching	widely separated	widely separated
Fastigium of vertex	flat or convex	sulcate or strongly compressed	convex or sulcate	flat, not sulcate
Lacinia	with 2 hook-like processes	with 3 hook-like processes	with 2 spiniform processes 1 minute	without any appendages
Tarsi	depressed, lobate	compressed, sclerotized, often with a minute pulvillus apically	compressed, pulvillate	compressed, pulvillate
Metatarsi	depressed, pulvillate	compressed, sclerotized	compressed with 2 pulvilli	feebly compressed, with 2 pulvilli
Tibial auditory tympanum	absent	absent	present or absent	absent
Wings	apterous or alate	apterous	great majority of species apterous	sexually dimorphic, males brachypterous
Sclerotization of tegmina	tegmina and wings soft, flexible	—	tegmina toughened	tegmina toughened
Femoro-abdominal stridulatory apparatus	present	absent	present	absent
Inserting angle of hind femur	present	absent	present	present, but minute

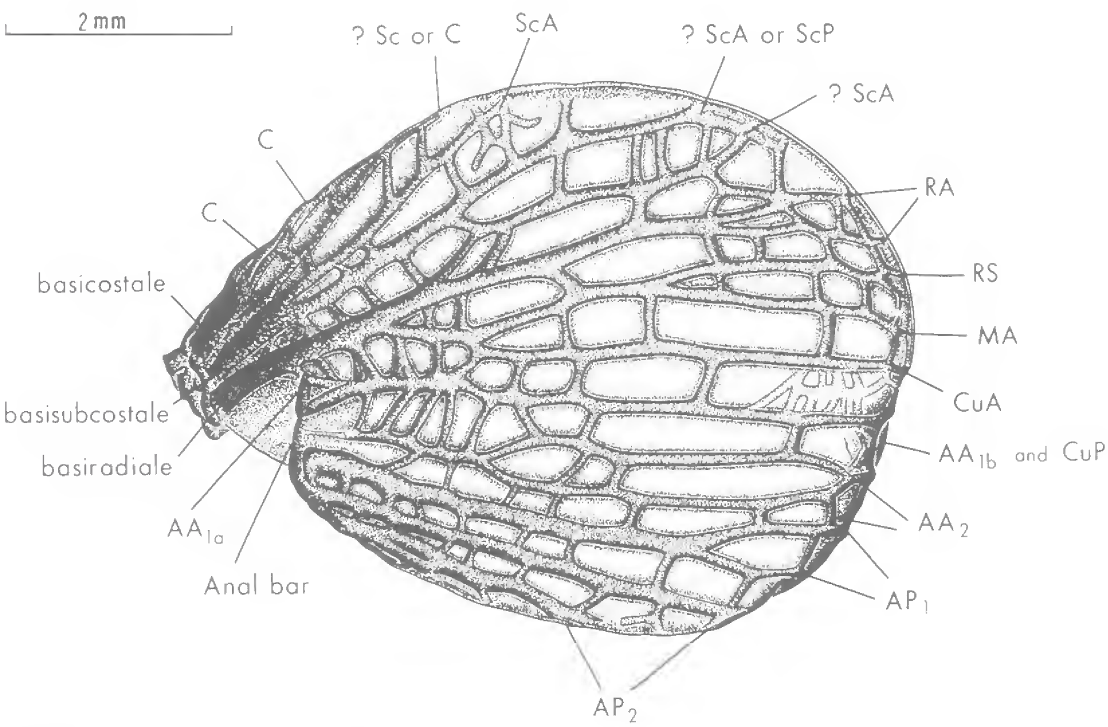

FIG. 8: Right tegmen of *C. propator*. Nomenclature after Kululova-Peck (1978).

The apex of the abdomen and the paraprocts are not modified but there are 2 pairs of digitiform hook-like, lightly sclerotized appendages on the genital orifice. These appendages are absent from *C. propator*.

In summary, it appears that *Oryctopus* is only superficially similar to *Cooloola*, the similarities being apparently associated with adaptation to a wholly fossorial habit. Since *Oryctopus* seems stenopelmatid in all but a few characters (most notably the reduced number of antennal articles and the piercing or cutting mouthparts) I feel that it should remain in the Stenopelmatidae, with the reservation that examination of additional material might lead to a change of its placement but that this would not affect the classification of the Cooloolidae.

Comparative Morphology of Selected Structures in the Cooloolidae

Wing Venation: The brachyptery and modification of the tegmen render identification of the veins difficult. A drawing of the tegmen was examined by Dr J. Kukalova-Peck who stated (in litt.) that she found it difficult to trace the homologies of the veins because of the sclerotization at the base of the tegmen. As a result, the origin of several of the veins is obscure. Some of the problems are as follows: it is not possible to determine with certainty whether ?C or Sc starts from the basicostale (and is therefore a part of the costal system) or from the basisubcostale (and is therefore part of the subcostal system); similarly with ?ScA or ScP the three branches may, in fact, be all ScA. In Figure 8 the veins in doubt are labelled with a query.

The venation of *C. propator* does not reflect relationship with any of the Haglidae, e.g. *Cyphoderris monstrosa* (see Sharov, 1971, fig. 25). Dr Kukalova-Peck feels that the venational characters are quite different and *C. propator* shows more primitive characters in the subcostal system but, conversely, reflects more advanced specialization in the anal field. The strong anal bar which is not present in the Haglidae, indicates that this area was more strongly developed in the past for some purpose, perhaps flight, burrowing, or courtship, but I am not now able to determine it. In sum, it can be stated that the venation of *C. propator* is quite distinct from that of any of the presently known orthopteroids and may indicate that the species is the sole survivor of a very archaic line of hitherto unknown orthopteroids.

Mouthparts: Mouthparts in Orthoptera, though variable, show adaptive modification based on the food preferences of the groups involved. Such was demonstrated by Gangwere (1965) for the North American Orthoptera. The mandibles of each subfamily, and often in groups below that level, are usually distinctive. Of all the mouthparts, the labium appears to remain relatively constant throughout the Orthoptera. The maxillae and labrum show a lesser degree of modification with the maxillae showing more substantial differences than the labrum (*contra* Isely, 1944, who stated that only mandibles show significant adaptive modification).

Because of the conservative nature of mouthparts, they can serve as a character for taxonomic differentiation. Gangwere (1965) was able to show that the tettigoniid subfamilies Conocephalinae, Copiphorinae, and Decticinae were more similar in the morphology of mouthparts, than to the Phaneropterinae of Pseudophyllinae. Such is an accepted fact based on more usual morphological characters.

Gangwere (1965) listed six kinds of mandibles for the Orthoptera. According to his scheme, *C. propator* fits the Carnivorous-Forbivorous or Flesh-Forb feeding subtype. The mandible is elongate and hook-like. The incisor and molar dentes are well defined and sharp, with the latter surrounding a minute but distinct concavity. However, his name of the subtype cannot be applied to *C. propator* since it appears unlikely that this insect feeds upon forbs. It is more probable that it feeds upon roots or organisms encountered underground. Other burrowing Orthoptera, such as mole crickets, have mandibles which are short and stout. They have well-defined molar regions designed for chewing rather than holding or tearing and they are classed in the Omnivorous category.

The mouthparts of *C. propator* are unique among the Ensifera in that the maxillae are larger and more prominent than the mandibles. The galea is small and slender and, as usual in Ensifera, lies above the lacinia. It is shorter than the lacinia, not apically modified and bears two rows of setae dorsally. This is in contrast to the Stenopelmatidae, Rhaphidophoridae and Gryllacrididae. In the first the galea is usually short and broad (see previous discussion for *Oryctopus* as exception). In the rhaphidophorids and the gryllacridids the galea is massive and its lateral and apical margins overhang the lacinia. The galea is a robust, quadrate structure and in the gryllacridids it is apically modified into a

sclerotized papillate sensory organ as is found in the Tettigoniidae. Laterally the galea possesses well-defined, although irregular, rows of setae.

The peculiar knife-like structure of the lacinia of *C. propator* (Fig. 9) is very different from that of the three related families. The lacinia of *C. propator* is unique in that it is modified to form a simple, broad, knife-like structure and bears no appendages. The dorsal surface has two minute tubercles at its broadest point, on the internal margin. Lateral to the tubercles lies a pair of pits, the internal pit is large and circular, the external minute. The apex of the lacinia is a smoothly bent cutting edge without hooks or teeth. Apically it is

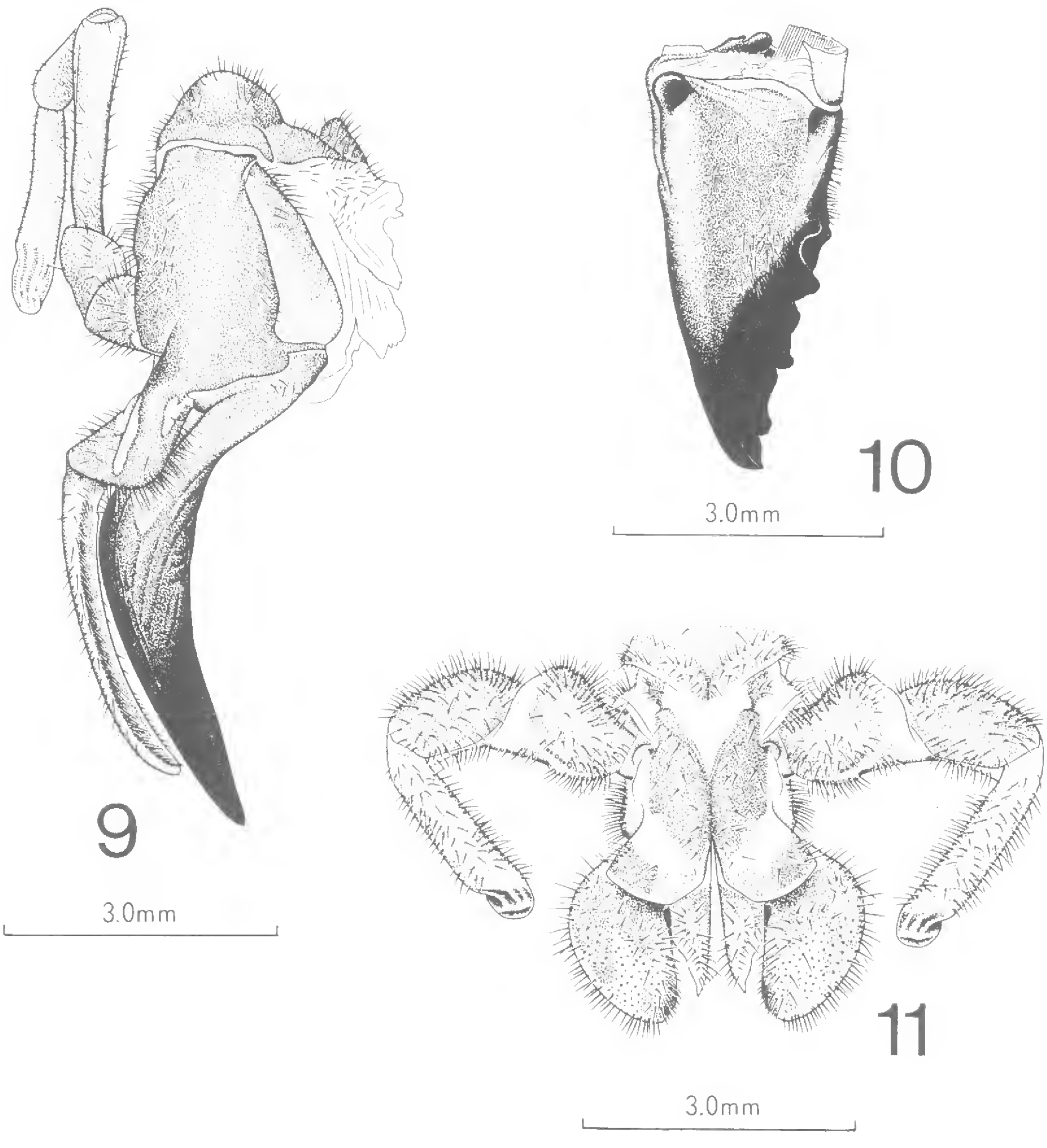

FIG. 9–11: Mouthparts, male paratype *C. propator*. 9, left maxilla: note blade-like lacinia; 10, left mandible: note elongate shape for grasping or tearing; 11, labium.

distinctly spatulate. In length it is half as long again as the mandible.

In the stenopelmatids the lacinia is dorsally tuberculate on the internal margin and bears at least two large tubercles on its dorsal surface. There is an elongate spiniform tooth on the internal margin at the base of the apical portion. A tiny spiniform tooth is found on the internal cutting edge of the lacinia itself. In the rhaphidophorids, the lacinia bears no tubercles and has three apical teeth. It shows no modification for cutting, but appears to have a tearing, or perhaps a sorting, function. The gryllacridids have an elongate non-tuberculate lacinia bearing two apical teeth on the internal margin. Near the proximal tooth lies an inconspicuous, short, stout spine.

The labrum and labium (Fig. 11) appear similar to those of other Orthoptera.

In general, the mouthparts of the Cooloola Monster suggest adaptation for piercing and chewing rather than chewing only, as is normal for Orthoptera. The reduced nature of the molar area (Fig. 10) and extraordinary development of the lacinia relative to the mandible supports this hypothesis. The structure of the gut also supports it. The enlarged foregut (see below) may be a modification for storage of liquid food and may explain the absence of solid food from the foregut in field-collected specimens. The reduced armature of the proventriculus may reflect its lessened function as a sieving mechanism. One can only speculate that the insects feed on insect larvae or, perhaps earthworms which are abundant in the habitat, or may feed on the toughened roots of trees and shrubs which lace the habitat.

THE ALIMENTARY TRACT: The alimentary canal was removed from one of the fluid-preserved specimens and studied as described by Judd (1948). For the sake of comparison, the terminology of structures follows that of Judd and his code is used in my illustrations. The alimentary canal of *C. propator* is peculiar in that the crop is extremely long and convoluted. The proventriculus lies in the posterior part of the abdomen, thereby by necessity, severely limiting the length of the midgut and hindgut. Although this is common in gryllacridids, stenopelmatids and *Cyphoderris* (Haglidae), it is not normal in tettigoniids or rhaphidophorids. In those families, the proventriculus lies in the thoracic region. Strangely, these differences were not registered by Judd. Perhaps some stenopelmatids, the cooloolids and *Cyphoderris* are sporadic and opportunistic feeders, feeding only occasionally when the situation warrants it, and then consuming large quantities of food.

Evidence suggests that sporadic feeding may depend on local weather conditions. Many of these insects are extremely sensitive to dry conditions and all are nocturnal. They may not venture forth each night unless atmospheric conditions are suitable. Such an explanation was offered for several species of the henicine stenopelmatid *Cnemotettix* of California which spend periods of dry weather in their burrows (see Rentz and Weissman 1973). At the same time Rentz and Weissman noted the extraordinarily large size of the faecal pellets of *Cnemotettix*. Curiously, however, I have found that the faecal pellets of certain other stenopelmatids and gryllacridids are very large. The same was also mentioned by Richards (1973, p.226) in the deinacridine stenopelmatid, *Hemideina* spp., the giant weta of New Zealand.

Comparative studies of the proventriculi of several examples each of the Tettigoniidae, Rhaphidophoridae, Stenopelmatidae, Gryllacrididae, Haglidae (*Cyphoderris*) and Grylloidea indicate that there is considerable overlap in the morphology of this structure from one group to the other. It appears that the taxonomic value of the proventriculus may lie at the generic level. However, a few generalisations can be drawn.

Based on the characters of the proventriculus, the Cooloola monster shows no similarities with any of the Grylloidea. In this group the median tooth normally has lateral projections and two lateral lobes. This is a more complex picture than exists in the Tettigonioidea and Gryllacridoidea. In these groups the general structure is simpler, the lateral teeth and inner barbate lobes of the sclerotized appendage of the proventriculus are absent. It thus seems that, on the basis of this structure, Sharov (1971) was wrong to transfer the Haglidae from the Tettigonioidea to the Gryllidea (= Grylloidea). He did this primarily on wing venation. Fresh preparations of the proventriculi of a species of the two extant genera of the Haglidae show none of the typical grylloid characters. Judd (1948), in an extensive survey of the Orthoptera, made a point that the Rhapidophoridae were distinct in that the median tooth of the sclerotized appendage of the proventriculus always bore a tuft of hairs. He illustrated this with several genera. However, I found in the rhaphidophorid *Macrobaenetes valgum* (Strohecker), a more or less typical example of the family from the southwestern

United States, there are no hairs at all. The lateral lobes, however, are lightly sclerotized as Judd indicated. He considered the proventriculi of the Stenopelmatidae, Tettigoniidae, and Prophalangopsidae (= Haglidae) indistinguishable from one another at the family level. With this I concur.

The most striking similarity of the proventriculus of the Cooloola monster is with that of *Cyphoderris monstrosus* Uhler. Judd did not illustrate an entire section of one of the longitudinal folds of the proventriculus of this important insect, but if he had it would have looked much like Fig. 13. He did illustrate the sclerotized appendage of the proventriculus (Judd 1948, figs. 73, 74) and the similarity with my Fig. 14 is, indeed, astounding. The most obvious differences between the proventriculus of *Cyphoderris* and *Cooloola* are the following: proportionally smaller size of proventriculus in *Cooloola*; much lesser degree of sclerotization; lack of distinct protuberances or modification of the cushions (Fig. 13) (C) of the sclerotized neck region in *Cooloola*; presence of tubular neck region in *Cooloola* (in *Cyphoderris* this is absent and the sclerotized portion of the neck is contiguous with the main portion); more angulate projection of the caudal portion of the barbated lobe (BL) in *Cyphoderris*; more lightly sclerotized loop of hairs (CT) in *Cyphoderris*. It can be concluded that in all aspects of the structure of the

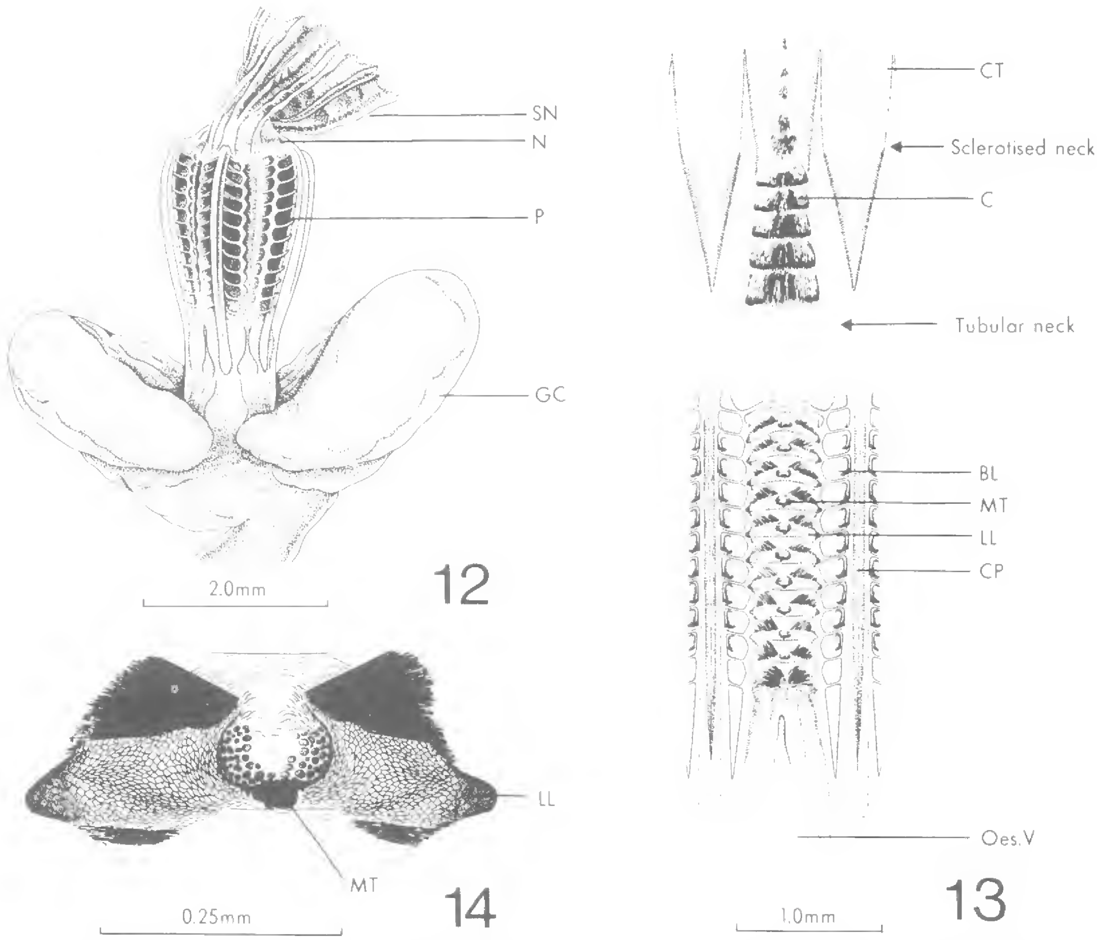

FIG. 12–14: Structures of foregut. Nomenclature after Judd (1948). 12, proventriculus, posterior end of crop and anterior end of midgut. SN = sclerotized neck, UN = tubular neck, P = proventriculus, GC = gastric caeca. 13, sclerotized portion of one longitudinal fold of proventriculus, CT = V-shaped loop of tubercules, C = cushion, BL = barbated lobe, MT = median tooth, LL = lateral lobe, CP = sclerotized partition, Oes.V. = oesophageal valve. 14, sclerotized appendage of proventriculus. LL = lateral lobe, MT = median tooth.

proventriculus, *Cooloola propator* shows more similarities with *Cyphoderris monstrosa* than any other ensiferan.

The proventriculus of *C. propator* is 2·2 mm long, and globular, it is joined to the crop by a tubular neck which is a distinctly unsclerotized zone. Where joined to the midgut, it is surrounded by two moderately large broad gastric caecae (GC). Beyond the constricted neck there are 5 or 6 longitudinal rows (Fig. 13) of poorly defined cushions composed of hairs. Each row of cushions appears faintly divided down the middle and consists of 5 well-defined pairs preceded by 3–5 smaller more poorly defined ones. The anterior cushions bear fewer hairs and are narrower. There is no median projection from any of the cushions. Between each row of cushions there is a V-shaped loop (CT) composed of minute tubercules. Each of the 6 longitudinal folds of the main part of the proventriculus consists of 10–12 sclerotized appendages. The median 5–9 are the widest and best developed, those on either end decreasing in size. Each longitudinal fold is spearated by a weakly sclerotized partition (CP) at the end of which there is a fleshy flap of the oesophageal valve (Oes.V.) which is not clothed with hairs. Each median appendage (Fig. 14) has a median tooth (MT) with minute tubercles at the base. There are no lateral teeth. From the side of each tooth are rows of extremely fine setae. Lateral to the seta is a minute blunt lateral lobe (LL). Each lateral lobe is bounded by a larger more quadrate barbated lobe (BL) which bears a blunt tooth posteriorly.

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PROCOELOUS CROCODILE FROM LOWER CRETACEOUS OF LIGHTNING RIDGE, N.S.W.

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ABSTRACT

Restudy of the type material and study of referred material of the Lower Cretaceous *Crocodylus (Bottosaurus) selaslophensis* indicates that the material is referable to neither *Crocodylus* nor *Bottosaurus*. Referred material includes procoelous cervical centra and suggests that the crocodile is an eusuchian. Distinguishing characters are a dentary with alveolar groove and medical shelf, procoelous cervicals, caudal transverse processes excavated posteriorly at their bases, and caudal neurocentral suture extending onto the transverse process. All known material derives from a small area of the Griman Creek Fm. at Lightning Ridge, New South Wales.

Crocodilian fossils are common in the Quaternary and late Tertiary of Australia (e.g. De Vis 1885; Longman 1924, 1925; Molnar 1976; Archer and Wade 1978; Gorter and Nicoll 1978). Miocene crocodilians, still largely under study, are also common at some localities. Earlier crocodilians have only rarely been reported in Australia. Riek (1952) reported crocodilian skin impressions (QUF 10625) from the probably Eocene Redbank Plains Series. These impressions show roughly hexagonal scales with distinct growth lines and lacking keels, a combination of features not known to occur in crocodilians. The general pattern of the scales could not be matched with that of any living crocodilian from the Australasian region, and thus it is unlikely that these skin impressions derive from a crocodilian. Riek (1952) also reported an angular from the Redbank Plains Series, thus demonstrating that crocodilians were present.

Etheridge (1917) described the earliest known Australian crocodile as *Crocodylus (Bottosaurus) selaslophensis*, from the Cretaceous opal-bearing beds at Lightning Ridge, New South Wales. While other crocodilian material from this site had already been obtained by the Australian Museum, Etheridge described only the type jaw fragment. Since 1917 further material has been discovered there, including procoelous cervical vertebrae. This material, like almost all found at the Ridge, was not in association, so it is possible that more than one taxon is involved. The duplicated left tibiae demonstrate that at least two individuals are represented. However all known material derives from individuals of approximately the same size, and among the latest discoveries I have seen teeth matching those in the type jaw indicating that elements possibly deriving from the same individual are still being found. In the absence of any indication that more than one taxon is represented, I shall assume that all pieces derive from a single species.

All fossil bones known from Lightning Ridge are opalized, at least in part, and thus many of the specimens have been retained by their discoverers and are represented in museum collections by plaster or resin casts.

Although Etheridge assigned the jaw fragment to *Crocodylus (Bottosaurus)* there is no indication in the literature that anyone else ever considered *Bottosaurus* a subgenus or a synonym of *Crocodylus*. Indeed *Bottosaurus* is usually classified (e.g. Steel 1973) as an alligatorine rather than a crocodyline.

COLLECTION DESIGNATIONS: AM — Australian Museum; QM — Queensland Museum; QUF — University of Queensland, Dept. of Geology.

Geology of Lightning Ridge

Nowhere at Lightning Ridge are there any extensive exposures of the opal-bearing beds. The geology of these beds has thus been interpreted entirely from features observed in the opal mines and the single large open cut and from the fossils collected from these mines. Earlier work on the stratigraphy of the Ridge (e.g. Whiting and Relph 1961) has been superseded by that of Byrnes (1977). He has concluded that the opal-bearing beds at the Ridge form the southern portion of the Griman Creek Formation which is more extensively exposed in southern Queensland. In New South Wales this formation is subdivided into two members, the Wallangulla Sandstone and the Coocoran Claystone. The opals (and fossils) occur in the Finch clay facies of the Wallangulla Sandstone Member.

Byrnes (1977) concludes that the Wallangulla Sandstone was deposited in estuarine conditions. In addition to fossil bone, pelecypods and gastropods have been found. None of the pelecypods represent clearly marine taxa (Byrnes 1977), while some of the gastropods are members of the family Viviparidae, which are fresh water forms. The occurrence of the fossil bones is such as to suggest transport: only in one instance were any found in articulation. Most of the elements seen are such as can be easily transported, e.g. femora, phalanges, teeth, centra, with no flat bones or ribs. The largest elements identifiable were plesiosaurian. Some of the bones appear to have been worn or broken prior to fossilisation, and one plesiosaur element had been bored. Plant material, including conifer cones, is reasonably common. Byrnes (1977) reports that some cross-bedding is present, and what appear to be impressions of plant roots occur in the clay facies. All of this suggests an estuarine environment of deposition.

Description

Mandible: Etheridge figured and described a fragment of crocodilian dentary with six teeth in situ (AM F15818) as the type of *Crocodylus selaslophensis* (Plate 1, E and G). The teeth are thecodont (as in all other known crocodilians) and not pleurodont as Etheridge stated: the bony partitions separating sequential alveoli are distinct. These partitions terminate below the level of the dorsal margin of the dentary so that the teeth are set in an alveolar groove. Slight anterior and posterior carinae are present on the crowns and striae are absent.

A medial shelf extends along the tooth row, giving the dentary the appearance of being wider than in *Crocodylus*. The lateral surface of the dentary is sculptured with longitudinal ridges and grooves much as modern *Crocodylus*. A prominent mass of opal along the medial surface (Plate 1, E) represents either a displaced bone fragment or an opalised mass of matrix, and not a projection from the dentary. There is no indication that this piece is from the symphyseal region as reported by Etheridge.

Maxilla: A small fragment (AM F18628) probably represents the anterior extremity of the right maxilla, with one tooth in place (Plate 1, F and H). Two other alveoli are present, one empty, the other occupied by only the root. The single crown is conical, medially flexed, and has fine striae but no carinae. The fragment as a whole is dorsoventrally compressed, suggesting a low, broad snout, and is lightly sculptured.

Cervicals: Two cervical vertebrae have been seen, the more complete represented by a cast (QM F9507), and the other a centrum in the Anderson collection that is also represented by a cast (QM F10240). Both centra are clearly procoelous, the anterior faces deeply concave, and the posterior convexities rimmed by a flange as in modern crocodilians. The posterior convexity of the Anderson centrum (Plate 2) is incomplete, and the anterior central face is worn, but appears to be slightly inclined upwards. This centrum is 18·5 mm long as preserved.

Both centra are constricted at the middle with marked ventral keels that descend anteriorly to form small, blunt hypophyses. Bases of both parapophyses and diapophyses are present on QM F9507 (Fig. 1), but absent from Anderson's specimen. The centrum of QM F9507 is 16·4 mm long, 15 mm high at the anterior face and 13 mm wide across that face. In general form and proportions both centra resemble cervical centra of the living species of *Crocodylus*.

Two portions of a cervical neural arch (AM F60081), although not sharing a contact, may derive from the same vertebra (Plate 2, D). Neurocentral articular facets, the base of the neural spine, the diapophyses, the left prezygapophysis and the base of the right are preserved. The arch is from a mid-cervical about 30 per cent larger than QM F9057. The neural spine is set anterior to the postzygapophyses, and both pre- and postzygapophyseal facets were more nearly horizontal than in *Crocodylus americanus* (Mook

1921, fig. 3). The arch resembles those of *Crocodylus porosus* in these features. The diapophyses are placed well above the neurocentral suture, as in the second cervical of *C. porosus*.

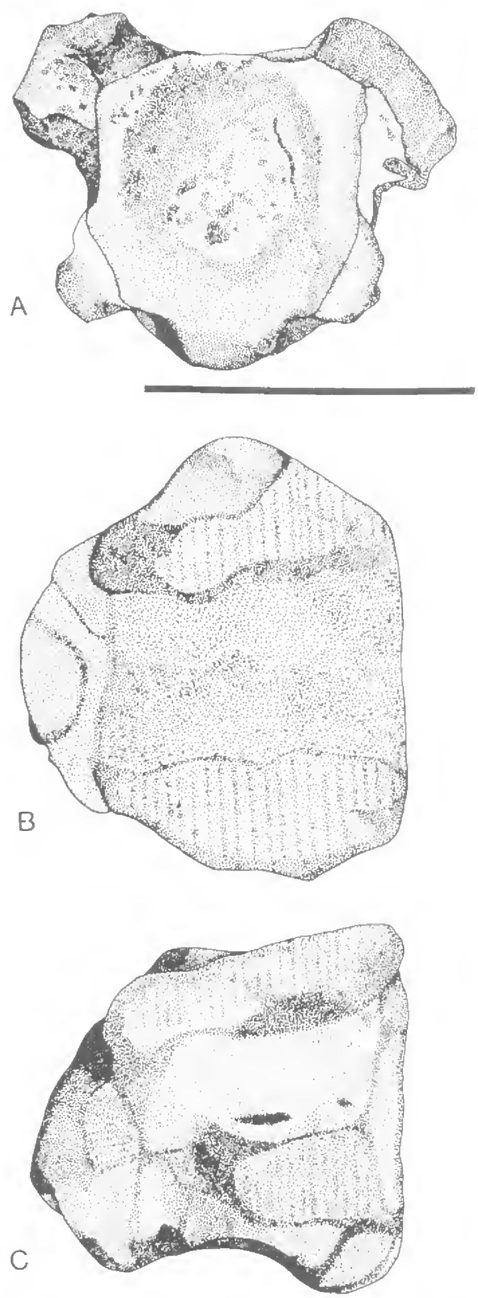

FIG. 1: Crocodilian cervical centrum from Lightning Ridge. (Specimen lost, represented by cast QM F8507.) Bar represents 2 cm. A, anterior view; B, dorsal view; C, lateral view.

SACRAL: The single sacral centrum (AM F15819) includes the lower portion of the neural arch with prezygapophyses, the entire left sacral rib and the base of the right (Plate 3). In general form this element greatly resembles the first sacrals of *'Leidyosuchus' multidentatus* (Mook 1930, fig. 5) and of *Diplocynodon hantoniensis* (Owen 1884, there given as *Crocodilus hastingsiae*). The prezygapophyseal facets are more nearly horizontal in this sacral than in the first sacral of either of these taxa, being inclined at only 25° to the horizontal. The anterior face of the centrum is shallowly concave, broad (23 mm wide by 12 mm high), and slightly inclined downwards. The posterior face is incomplete, less broad, almost flat (with but a shallow central concavity) and is slightly inclined dorsally. The centrum is 24 mm long, as is the sacral rib which bears a posteriorly inclined iliac articular surface. A distinct ridge extends from the prezygapophysis laterally along the anterodorsal edge of the rib. The ventral surface of the centrum is faintly concave with slight longitudinal ridges along both sides.

CAUDAL: The proximal caudal centrum (AM F60080) includes portions of both diapophyses and the right prezygapophysis (Pl. 2), and is 28 mm long, 13 mm high and 12 mm wide at the anterior face. The central articular faces are inclined as in the single known sacral. The centrum is constricted at the middle, with two sharp ventral keels much like those of the caudals of *Holopsisuchus brevispinus* (Cope 1869, Pl. IV, fig. 4). Both central faces are concave as preserved, but both are worn so it is not certain that the centrum was amphicoelous. The neurocentral suture was dorsal to the diapophyses and zygapophyses and extended laterally 12 mm onto the dorsal surface of the transverse process. A distinct pocket extends into the posterior margin of the transverse process just lateral to the postzygapophysis.

CERVICAL RIB: The proximal portion of a cervical rib (AM F60082), from the left side, does not differ from those of *Crocodylus porosus*.

FEMUR: An incomplete element possibly representing the distal one-third of a right femur is present in the collection of K. Barlow (Plate 1, A and B). The specimen is badly worn, but has less curvature in the shaft than femora of *Crocodylus*.

TIBIA: Two left tibiae are preserved, the distal end missing from both. The smaller (AM F18630) is less than 10 per cent smaller than the larger (AM F15821) (Plate 1, C and D). In both the cnemial crest is badly worn. These two tibiae are identical and closely resemble those of *C. porosus*, from which they differ only in that the lateral surface of the shaft is flat with a sharper anterolateral border and a less marked posterolateral border.

DISCUSSION

Etheridge's type specimen (AM F15818), a dentary, is characterised by: 1) an alveolar groove and 2) a medial shelf. Assuming that the other crocodilian material is referable to the same taxon, it is further characterised by: 3) a low, probably broad snout; 4) procoelous cervicals, with a small hypophysis; 5) keeled caudal centra; 6) excavated caudal diapophyses; and 7) caudal neurocentral suture extended onto diapophysis. Postcranial elements resemble those of crocodylids in the forms of the cervical and sacral vertebrae, and of the tibia. This general resemblance, together with the procoelous character of the cervical centra, suggests that this crocodilian was eusuchian.

The type jaw fragment of *Crocodylus selaslophensis* was compared by Etheridge with a jaw fragment referred to *Bottosaurus harlani* (most recently figured by Mook, 1925, fig. 8). The latter specimen is attributed to an immature individual. There is no clear evidence of immaturity of the Lightning Ridge crocodile, although the caudal neural arch has separated from the centrum at the neurocentral suture, as has the cervical neural arch (but not that of the sacral). Mature teeth of *B. harlani* are considerably more bulbous and blunt than in the Lightning Ridge form, and neither the type jaw of *B. harlani* nor the referred immature specimen exhibit an alveolar groove. Thus the Lightning Ridge crocodilian is not referable to *Bottosaurus*.

The alveolar groove and the excavated caudal transverse processes suggest that this form is also not referable to *Crocodylus*. The genus *Crocodylus* is not otherwise known to range into the Lower Cretaceous (cf. Steel 1973), and the three reported Lower Cretaceous English species (*C. cantabrigiensis*, *C. icenicus*, and *C. saulii*) have not been reviewed since the nineteenth century and are of uncertain significance. *C. saulii* may be congeneric with *Bernissartia fagesii* (Buffetaut, 1975).

Other than *'Crocodylus' selaslophensis*, only two crocodilians exhibit an alveolar groove: *Edentosuchus tienshanensis* (Young, 1973) and *Macelognathus vagans* (March 1884, Ostrom 1971). Both are currently referred to the Mesosuchia, and both differ from the Lightning Ridge crocodile (and from each other) in several other characters; no close relationship is warranted.

Procoelous vertebrae, considered characteristic of eusuchians, also occur in a mesosuchian (Joffe 1967), and reportedly in a sebecosuchian (Arid and Vizotto 1965). The mesosuchian is *Theriosuchus*, an atoposaurid. Atoposaurids have been suggested as possible ancestors of eusuchians (Joffe 1967; see also Langston 1973). However the known atoposaurids are all considerably smaller than the individuals represented at Lightning Ridge and all date from the Upper Jurassic. None are reported in the literature to exhibit excavated caudal diapophyses, an alveolar groove, or several of the other characters of the Lightning Ridge crocodile. In the absence of further evidence it may be assumed that the Lightning Ridge crocodilian is not a large atoposaurid.

The sebecosuchian *Baurusuchus* also reportedly had procoelous vertebrae (Arid and Vizotto 1965). The type jaw and maxillary fragment from the Ridge show none of the dental specializations of sebecosuchians, so that reference to this group can also be ruled out. Unfortunately the vertebrae of *Baurusuchus* were not illustrated so that comparison of the vertebrae cannot presently be made.

The occurrence of a procoelous crocodilian in the Lower Cretaceous (Aptian or Albian) of Australia is unexpected. *Hylaeochampsa vectiana*, usually recognised as the earliest known eusuchian (Romer 1966, Steel 1973), comes from the Lower Cretaceous of England. The Lower Cretaceous *Bernissartia fagesii*, often considered eusuchian (e.g. Charig 1967) has recently been demonstrated to be a mesosuchian (Buffetaut, 1975). *Heterosuchus valdensis*, also from the Lower Cretaceous of western Europe, is often considered congeneric with *Hylaeochampsa* (Romer 1966, Steel 1973). While *Hylaeochampsa* is known only from cranial material, *Heterosuchus* is known from postcranial material, including procoelous vertebrae. The three Lower Cretaceous species attributed to *Crocodylus*, as mentioned previously, need restudy. The described vertebrae of *C. cantabrigiensis* and *C. icenicus* are procoelous, and generally resemble those from Lightning

Ridge (Seeley 1874, 1976). All these forms are from western Europe.

The earliest extra-European eusuchians (*Aegyptosuchus, Stomatosuchus,* and *Stromerosuchus*) appear in North Africa around the Cenomanian, although a procoelous vertebra has been found in the Albian of Algeria (Buffetaut pers. comm., 1979) and by the latest Cretaceous eusuchians were widespread and diverse. Thus the indication of a possible eusuchian in the Aptian or Albian of New South Wales suggests a considerably wider range of procoelous crocodilians during the Lower Cretaceous than has been generally recognised.

The holotype of Etheridge's *Crocodylus* (*Bottosaurus*) *selaslophensis* is too incomplete for confident comparison with other specimens. However it is sufficiently unique (see the character states listed on p. 136) that should more complete material be found, the taxon would be both recognisable and diagnosible. Further, the Griman Creek Formation has been so little explored for fossils that it is premature to relegate Etheridge's species to the status of *nomen vanum* until it is clear that more complete topotype material is not forthcoming.

SUMMARY

Procoelous cervical vertebrae from the Griman Creek Fm. (probably Albian) of Lightning Ridge, New South Wales, demonstrate the existence of a procoelous crocodilian in Australia during the Lower Cretaceous. Assuming that all the remains pertain to a single taxon, that taxon is characterised by procoelous cervicals, excavated caudal transverse processes and caudal neurocentral suture extending onto the transverse processes. This material probably pertains to *Crocodylus selaslophensis* Etheridge (1917). The type dentary fragment of that species has an alveolar groove and a medial shelf establishing that there is no reason to refer this species to the genus *Crocodylus*. The species is regarded as indeterminate pending the discovery of further material from the Griman Creek Fm.

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PLATE 1

A: Distal end of ?femur from Lightning Ridge (Barlow collection) posterior aspect.

B: The same, medial aspect. Bar represents 1 cm.

C: Crocodilian tibia from Lightning Ridge (AM F15821) medial aspect.

D: The same, anterior aspect. Bar represents 2 cm.

E: The mandibular fragment (holotype) of *Crocodylus (Bottosaurus) selaslophensis* (AM F15818), dorsal aspect.

F: Crocodilian maxillary fragment from Lightning Ridge (AM F18628), lateral aspect.

G: The mandibular fragment, lateral aspect. Bar represents 1 cm. Unbroken surface is present around the specimen beneath the third and fourth teeth, thus the full depth of the mandible is represented at that point.

H: The maxillary fragment, ventral aspect. Bar represents 1 cm.

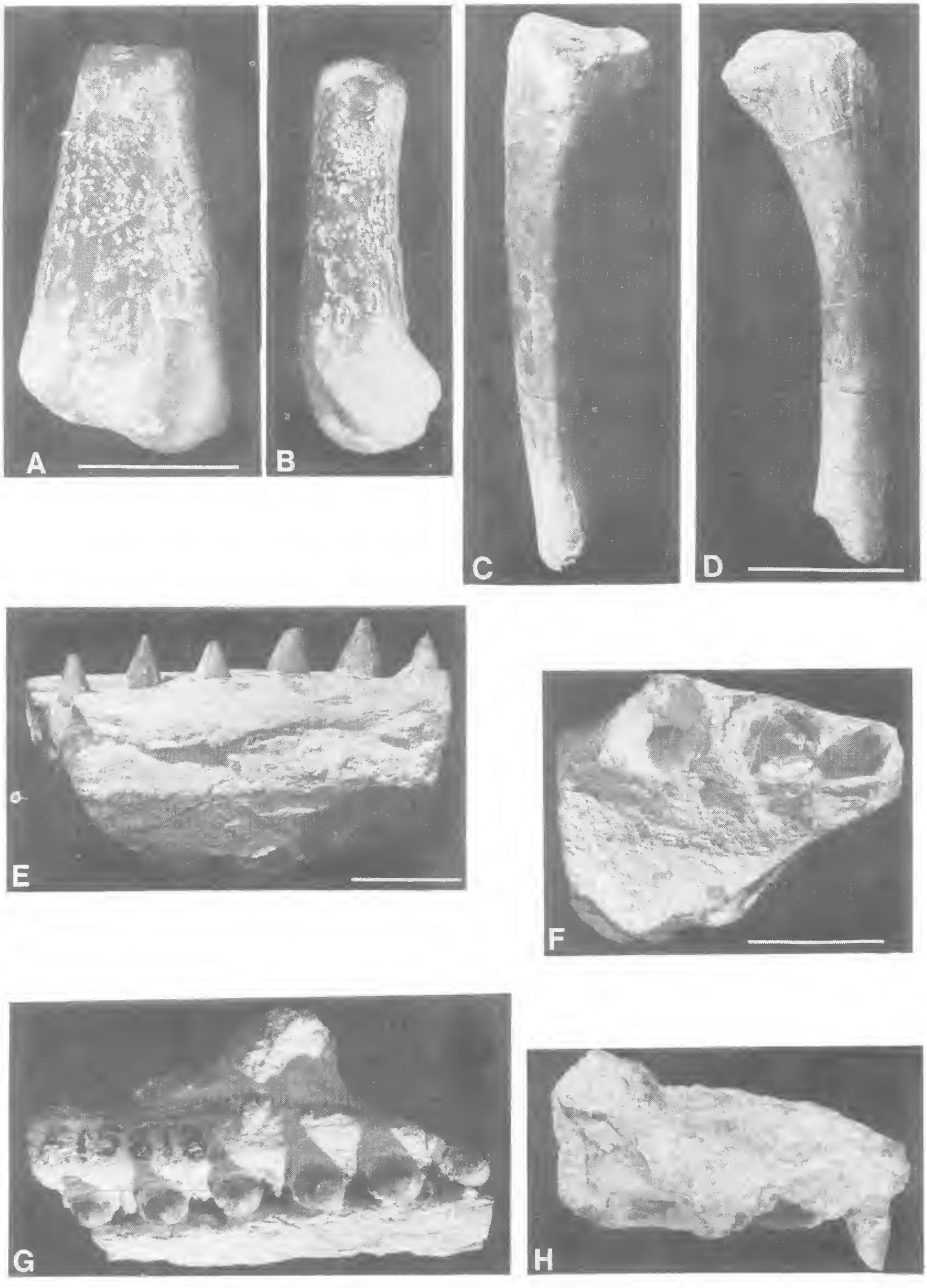
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PLATE 2

A and B: Crocodilian cervical centrum from Lightning Ridge, A, dorsal and B, lateral aspect of centrum in the Anderson collection. Bar represents 2 cm.

C: Crocodilian caudal vertebra from Lightning Ridge (AM F60080) lateral aspect. Bar represents 2 cm.

D: Incomplete cervical neural arch of crocodilian from Lightning Ridge, anterior aspect (AM F60081). Diagonal hatching indicates glue connecting the two portions. Bar represents 2 cm.

E: The caudal vertebra (AM F60080), ventral aspect.

F: The same, dorsal aspect.

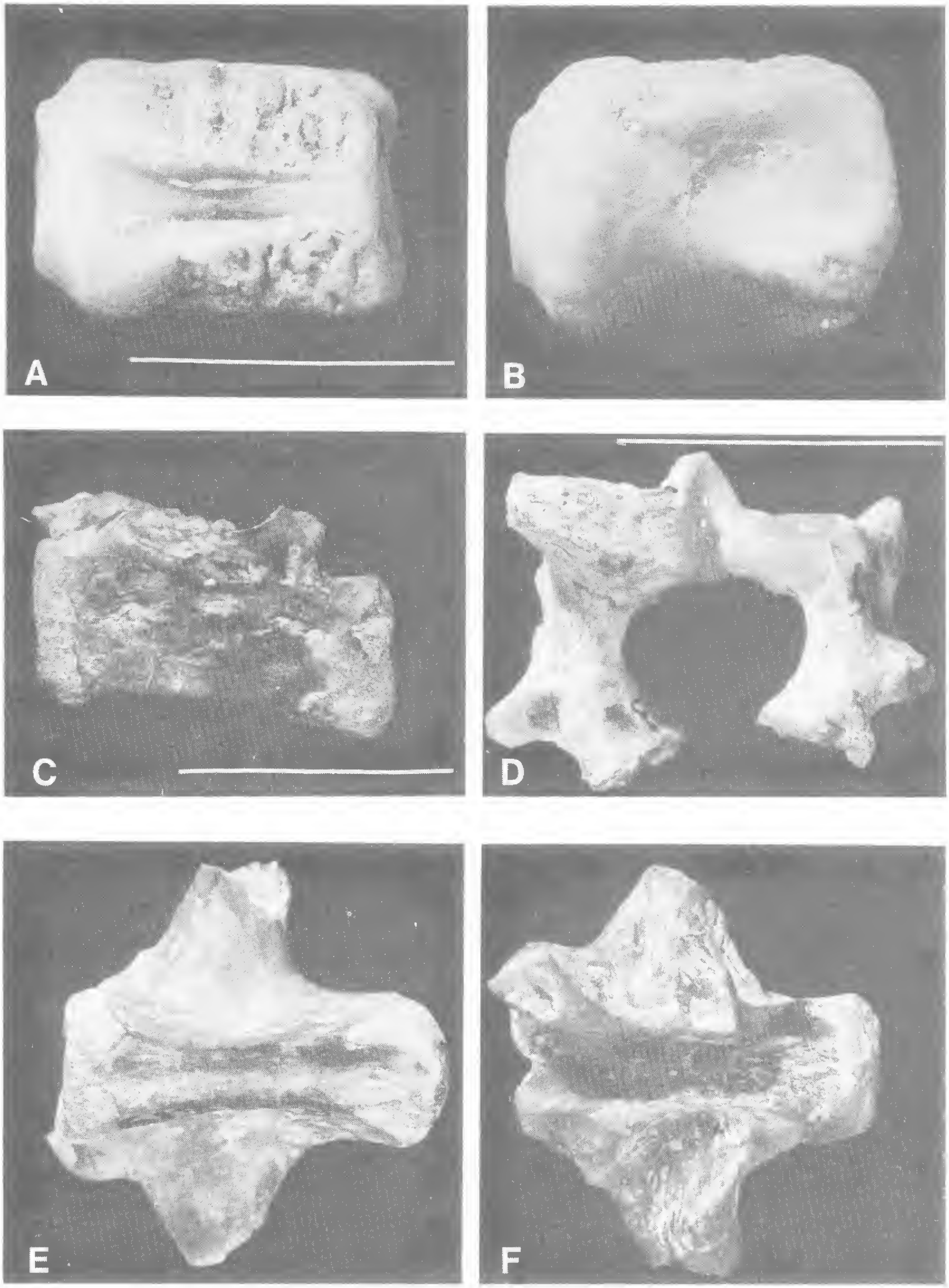
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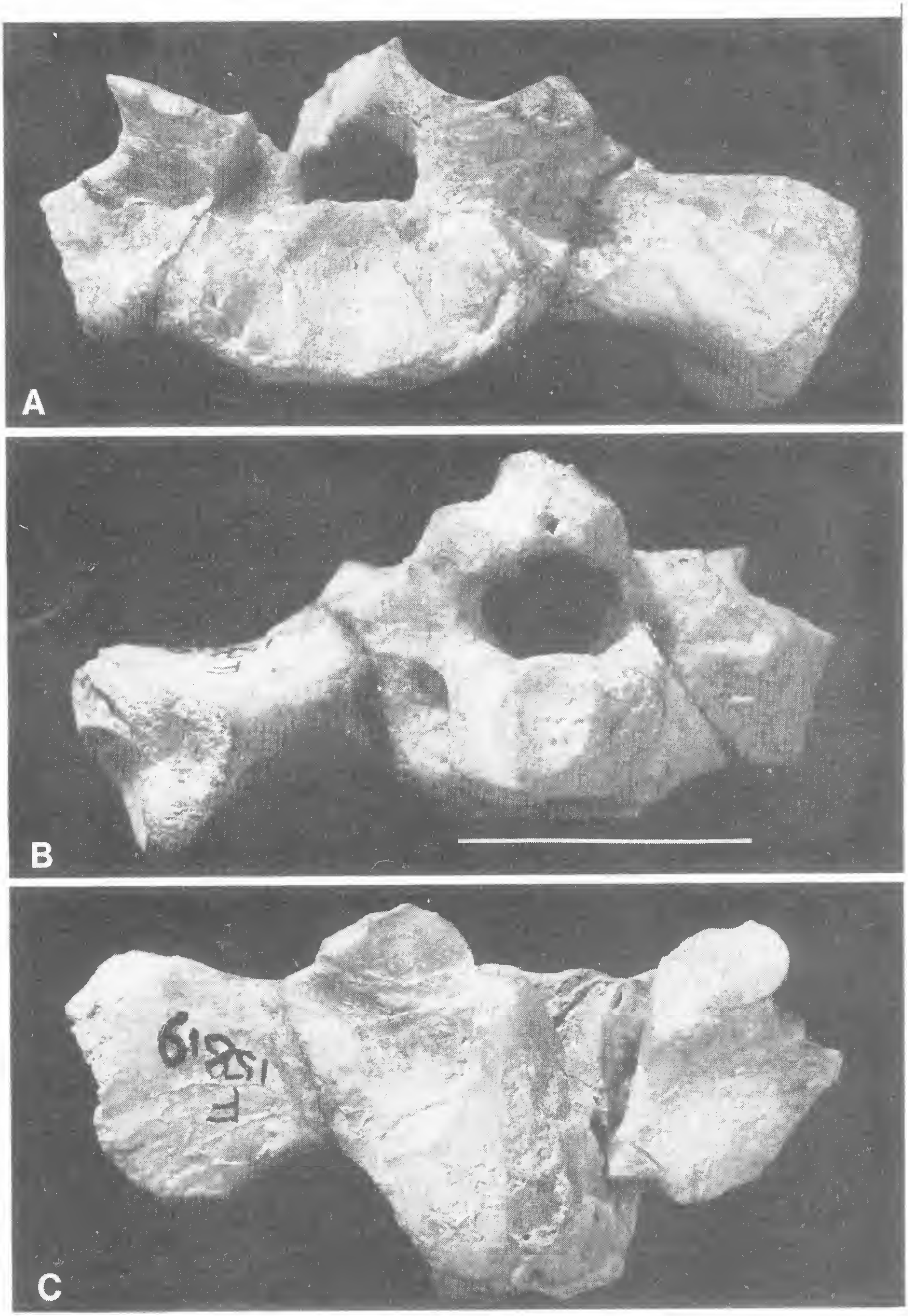
PLATE 3

A: Crocodilian sacral vertebra from Lightning Ridge (AM F15719) ventral aspect.

B: The same, posterior aspect.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AN ANKYLOSAUR (ORNITHISCHIA: REPTILIA) FROM THE LOWER CRETACEOUS OF SOUTHERN QUEENSLAND

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ABSTRACT

A small ankylosaur, described as a new genus and species *(Minmi paravertebra)*, has been found in the Lower Cretaceous Bungil Fm. near Roma, southeast Queensland. The specimen is unique in the possession of a ventral armour of small ossicles, and possession of bony elements alongside of the neural spines of the dorsals, herein called paravertebrae. This is the first ankylosaur discovered in Australia.

The ankylosaurs include the prominent armoured dinosaurs of Cretaceous times. Well known specimens have been found in Asia, North America and Europe, but little is known of this group in the southern hemisphere (e.g. von Huene 1929, Nopcsa 1929). Two reports of armoured dinosaurs from Australia (Etheridge 1904, Bartholomai 1966a) have proved incorrect. The earlier was due to a misidentification of bivalve steinkerns, and the latter to a misidentification of sauropod limb material. The specimen described herein thus represents the first ankylosaur known from Australia, as well as the most complete material yet described from the southern hemisphere (although admittedly incomplete compared with much northern hemisphere material).

In addition to its geographic significance, this specimen is the first to show extensive regions of the ventral armour. The presence of a series of previously undescribed ossifications alongside of the neural spines of some posterior dorsal vertebrae is also clearly demonstrated.

The specimen consists of eleven dorsal vertebrae and associated elements, an incomplete right pes, and much of the ventral armour, and was collected by Alan Bartholomai in 1964 probably from a gulley 1 km south of Mack Gulley, north of Roma, Queensland. The material was preserved in calcareous concretions, and was articulated when discovered.

STRATIGRAPHY

The site lies on the mapped Minmi Member of the Bungil Formation (Day 1964, Exon and Vine 1970). This member consists of medium to fine sands, silts and muds, with calcareous concretions (Day 1964, Exon 1976), and was deposited under freshwater (Day 1964) or brackish marine conditions (Exon 1976). No other vertebrate material is known from this unit, which is considered of Lower Cretacous age, probably Aptian (Exon and Vine 1970), although dates as early as Neocomian have been suggested (Exon 1976).

OCCURRENCE

At least the trunk and pes of the creature were articulated when it was buried, and the ventral armour was still in position. Some wear, breakage, and displacement of elements did however occur, with one instance of considerable re-orientation. The proximal portion of the left(?) rib associated with the sixth vertebra from the front preserved, was displaced, rotated about 180 degrees and came to rest across the posterior central articular face. The other instances of breakage did not result in such re-orientation, usually with no movement of the detached portion. All of the left ribs, except that fused to the vertebra, have been ventrally displaced as a unit, and some of the vertebrae have also slipped downwards.

In addition to yielding the osseous remains, the matrix of the concretions showed some other structure. The texture of the matrix varied across the pavement of ventral scutes, and was uniformly argillaceous external to the pavement, but with large regions of coarser grain size internal to that layer. These regions formed no discernible pattern within the concretion. Large, lobate masses of clay also occurred between the level of the vertebral column (and ribs) and that of the ventral ossicles. Unfortunately because of the fragmented condition of the concretions no overall pattern of these clay masses was discernible. There appears to have been a sheet of clay below the vertebrae, with other possible isolated masses lying just above the ventral pavement. The sheet is considerably thinned beneath the vertebral column and deflected upwards on either side of the row of centra, as if, after formation of the sheet, the vertebral column had subsided into it. While it is tempting to identify these clay masses with some visceral structure there is no good evidence for this. The obvious structures that might be filled with clay would be the lungs or the gastrointestinal tract. The continuity of the sheet from one side to the other beneath the vertebral column suggests that it does not represent a fill of the lungs, and the great breadth of the sheet, together with the absence of any internal structures that could possibly be attributed to ingested food, suggests that a fill of the gut tract is likewise not represented.

Five ossicles from the ventral pavement, together with one small, water-worn quartz pebble, were found between the ventral pavement and the level of the ribs and vertebrae. This relocation of the ossicles suggests that they fell to these positions from the ventral pavement while the carcase lay upside-down on the substrate.

IDENTIFICATION

Although ankylosaurs have been recovered from marine deposits (e.g. Mehl 1936), the occurrence of an incomplete specimen on a continent not previously known to yield ankylosaurs requires justifying this identification. Eight groups of Mesozoic reptiles are known to have developed extensive dermal armour: chelonians, placodonts, aetosaurs, phytosaurs, crocodilians, sauropods, stegosaurs, and ankylosaurs. Three of these, the placodonts, aetosaurs, and phytosaurs, are not known to have survived the Triassic, and also differed in the form of the ventral armour and vertebrae from the Minmi saurian. Chelonians are characterised by the development of a ventral plastron rather than a pavement of ossicles, and by fusion of the ribs to the carapace, a feature absent in the Minmi saurian. Eusuchian crocodiles have procoelous dorsals, which the Minmi saurian does not, while mesosuchians have more nearly horizontal transverse processes and zygapophyses than the Minmi saurian. When armoured, mesosuchians have broad ventral plates rather than a pavement of small ossicles. Most sauropods apparently did not possess dermal armour, but recently discovered material from Argentina (Bonaparte, Salfity, Bossi and Powell 1977) does exhibit an armour of small ossicles, resembling those of the Minmi saurian. The first sacral of this form is opisthocoelous (Bonaparte and Powell 1978) and this suggests opisthocoelous dorsals, while those of the Minmi saurian are amphiplatyan. Stegosaurs have elongate, elevated dorsal neural arches quite unlike those of the Minmi saurian, and the spines or arches are posteriorly inclined, while those of the Minmi saurian are vertical.

Thus the Minmi saurian may be excluded from seven of these eight groups, the ankylosaurs alone remaining. The Minmi saurian shows several ankylosaurian features, such as a presacral rod, fusion of ribs to vertebra, centra with expanded amphiplatyan articular faces, and transverse processes inclined dorsally (Coombs 1978), and therefore the Minmi saurian is considered an ankylosaur.

In spite of the incompleteness of the specimen, which does not render it ideal type material, the unique features represented (ventral armour and paravertebrae) make it desirable to provide a name for this taxon.

Order ORNITHISCHIA Seeley
Suborder ANKYLOSAURIA Osborn
Family *incertae sedis*
Genus *Minmi* nov.

TYPE SPECIES *Minmi paravertebra* nov.

DIAGNOSIS: Small ankylosaur with paravertebral elements present; ventral armour formed by a pavement of small ossicles; dorsal vertebrae amphiplatyan, without notocordal knobs; transverse processes slender and triangular, not T-shaped, in section; neural canal broad; posterior intervertebral notch shallow.

ETYMOLOGY: *Minmi* from the Minmi Crossing, near the site of discovery. 'Minmi' seems to be of aboriginal origin, but uncertain meaning, either being a corruption of Min Min (a kind of will-o-the-wisp light), or referring to a large lily (Reed 1967).

Justification of the erection of a new genus for this specimen presupposes knowledge of the detailed description. Thus this justification is postponed to the discussion.

Minmi paravertebra nov.

TYPE SPECIMEN: Queensland Museum F10329. Eleven dorsal vertebrae, with associated bases of eleven ribs and three paravertebrae; five incomplete ribs; one incomplete pes; ventral armour; two unidentified elements.

LOCALITY: Probably a gulley about 1 km south of Mack Gulley, on the Injune Road, north of Roma, southeast Queensland.

HORIZON: Minmi Member of the Bungil Formation.

AGE: Lower Cretaceous, probably Aptian.

ETYMOLOGY: The specific name refers to the unique paravertebral elements.

DIAGNOSIS

As there is only a single species attributed to the genus, the specific diagnosis cannot be separated from the generic diagnosis.

DESCRIPTION

VERTEBRAE: Eleven vertebrae are preserved. They were all articulated, but are not demonstrably consecutive. They were collected in two groups of three, and one of five. Most retain both centra and arches, while four retain the transverse processes (of at least one side) and the spines as well. The two most posterior centra of the group of five are fused together with no sign of exostoses or other pathological features, and thus this is identified as the anterior end of the presacral rod.

The centra are uniformly amphiplatyan, without notocordal knobs. They are laterally and ventrally constricted, with expanded articular faces. These faces are subcircular without obvious compression. Slight lateral depressions are found in the centra just below the pedicles of the arches. Only one centrum has a keel, and it is faint. (Plate 1, fig. B).

The neural arches are but slightly elevated (Fig. 1). The neural canals are high but broad, the ratio of breadth to height ranging from 0·76 to 1·02. The transverse processes are slender, dorsally inclined, and triangular (not T-shaped) in cross-section. The diapophyseal facets face ventrolaterally, and are situated just below the ends of the processes, giving the tips an unswept look when viewed from the front or back. These facets are shallowly concave, and just dorsal to them, at the tips appear smooth, shallowly convex surfaces like articular surfaces. The parapophyseal facets are cuplike, and situated on the arches at the level of the top of the neural canal. No variation in this level is apparent, however on the posterior vertebrae a rugose band joins the parapophyseal to the diapophyseal facet, running along the ventral margin of the transverse process. The parapophyseal facets are each backed by a buttress supporting the transverse process and running ventrally onto the centrum. A second buttress runs posteriorly along the top of the postzygapophyseal facet.

The neural spines are uniformly thin, rectangular and anteroposteriorly long. They overhang the posterior ends of the centra. The prezygapophyses are borne on short processes that, however, increase in length posteriorly. The facets are inclined at about 65 degrees to the horizontal and are united along their ventral edges to form a V-shaped trough. The postzygapophyses are borne directly on the overhanging posteroventral portion of the neural spine.

PARAVERTEBRAE: On the left side of the first three of the group of five vertebrae preserved in articulation, are a set of three posteroventrally inclined, elongate bony rods. These rods superficially resemble those identified as ossified tendons, but one may be seen to attach to the

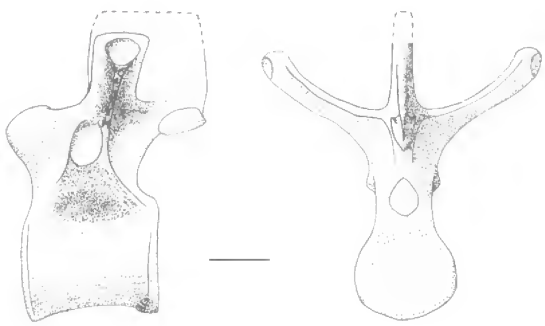

FIG. 1: Dorsal vertebra of *Minmi paravertebra* in left lateral (left) and posterior (right) aspects. Broken line indicates reconstructed portion. Bar represents 2 cm.

posterior margin of one of three elements located between the neural spines and the tips of the right transverse processes. Such elements have not been previously reported, and are here called paravertebrae (Plate 1, figs. C and D). These paravertebrae are flattened and lie in the horizontal plane (Fig. 2). The rod-like processes, all incomplete posteriorly, extend back at least the length of one vertebra, and attach to the posteromedial corner of the paravertebra. The anterior two paravertebrae are triangular in form when viewed from above, with the posteromedial angle a right angle, and the hypotenuse shallowly emarginate around the tip of the transverse process. This margin is serrate. The posteriormost paravertebra is elongate, extending well lateral to the tip of the transverse process, and appears to have been rectangular in form when viewed from above. The medial margins of both this and the middle paravertebra are deflected ventrally to lie along the lateral faces of the neural spines.

The dorsal face of the posteriormost paravertebra is preserved (the others are eroded dorsally) and shows no sign of sculpture as is found in dermal armour. Mantell (1851) reported that *Hylaeosaurus* had a row of small ossicles on either side of the neural spines. In *Euoplocephalus tutus*

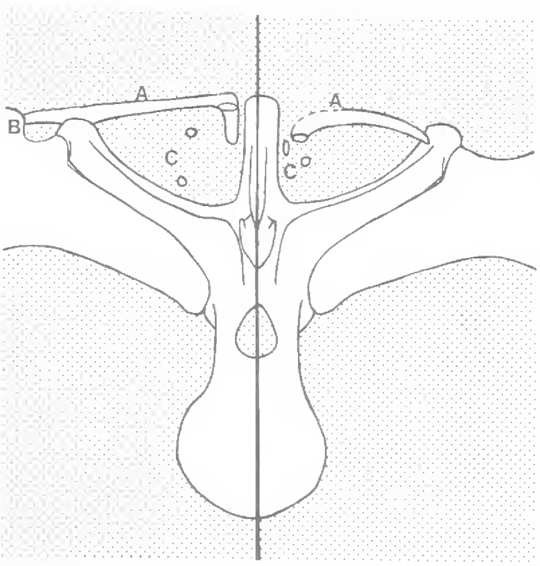

FIG. 2: Posterior dorsal vertebrae, ribs and paravertebrae in posterior aspect: posteriormost vertebra preserved on right, preceding vertebra on left. A, paravertebra; B, dorsal process of rib; C, presumed ossified tendons.

(the specimen originally described as *Scolosaurus cutleri*) the dorsal tips of the neural spines extend up to the plane of the dorsal armour, as may be seen in Plate 7 of Nopcsa (1928). Thus the paravertebrae may have been situated in the plane of the dorsal armour, since they are at the level of the tops of the neural spines, but there is no evidence that they either formed part of the dorsal armour or supported elements of the dorsal armour.

Maryanska (1977) describes a set of plate-like processes attached to the ribs in *Saichania chulsanensis*. These processes, which attach to the posterior margins of the distal portions of the ribs, are obviously not paravertebrae which are found proximal to the tubercles of the ribs and are not known to attach to the ribs at all. Nonetheless these processes, which Maryanska also believes may have been present in *Ankylosaurus* and *Panoplosaurus (= Edmontonia)*, as well as the paravertebrae, exemplify a tendency among the ankylosaurs toward the development of (presumably) dermal plates in the body wall.

The existence of the elongate posterior processes suggests some attachment of the dorsal epaxial muscles to the paravertebral elements, and hence mobility of the paravertebrae relative to the vertebrae. If the paravertebrae were associated with armour this could imply mobile dorsal dermal armour. The adaptive advantage of this is obscure. The posteriormost paravertebra extends sufficiently far laterally to reach the rib, and could thus have contacted it. The other paravertebrae preserved, however, seem not to have reached their respective ribs, so that any arrangement resulting in rib motion would seem to have affected only one pair of ribs. In conclusion while the paravertebrae may well have exhibited some limited motion relative to the vertebrae, the function of this motion cannot be presently stated.

Two short rod-like segments inclining posterodorsally lie against the neural spines medial to the elongate processes: these seem to represent actual ossified tendons.

RIBS: The bases of eleven ribs are preserved along the left side of the dorsals, but only of three on the right, the others having been lost due to erosion. Portions of the more distal regions of five successive ribs are also present.

The bases of the ribs are strongly compressed anterolaterally and the capitulum is bluntly convex and dorsoventrally elongate. The tuberculum is a low, convex facet on the medial side of the low tubercle. On at least one rib these two

facets are connected by a thin, shallow trough, suggesting a continuous articulation with the vertebra as is found in some other ankylosaurs (Coombs, pers. comm.). One fragment of rib shows the edge of a marked, medially recurved dorsal process lateral to the tubercular process (Plate 1, fig. E); unfortunately the rib is broken at this point so that the extent of the process is not known. The other proximal portions of ribs are all broken just lateral to the tubercular process.

More distally the ribs take on the characteristic T-shaped cross-section of ankylosaur ribs (also found in some sauropods and some hadrosaurs, Gilmore 1914).

PES: Three metatarsals, four phalanges (including an ungual) and a single tarsal remain of the right pes. (Plate 1, fig. A). The disposition of the metatarsals and phalanges indicates that at least four digits were present. The ventral portions of all of the pedal elements are badly worn. The tarsal could not be identified, and is irregularly quadrangular in form. The metatarsals are robust, expanded proximally, and constricted at mid-shaft. The ungual is blunt and about 1·5 times as long as wide.

VENTRAL ARMOUR: The preserved ventral surface is covered by a pavement of small dermal ossicles. This surface is apparently from the belly just anterior to the pelvis, as the portions of the pavement were preserved on the same blocks as the dorsal vertebrae. The ossicles are uniform in size and shape, small, 6 to 8 mm in diameter and 4 to 5 mm thick. They are cushion-shaped, flattened, roughly hexagonal to roughly square in form from below. The dorsal (internal) surface exhibits the common surface texture of trabeculae running in two mutually perpendicular directions, described for *Nodosaurus* by Lull (1921). The ventral (external) surface is mildly sculptured in a radiate pattern; there is no indication of any keel. The ossicles occur in a single layer and there is no obvious variation in size or form. A flat, roughly triangular, badly weathered element, 6·5 by 5 cm as preserved was found 5 mm above a fragment of rib. This piece may indicate a dorsal armour composed of scutes larger than those found on the venter.

DISCUSSION

COMPARISON: Comparison of *Minmi* with the known taxa of ankylosaurs must be based on vertebral form, since paravertebrae are absent in the other taxa, the ventral armour is either missing or poorly preserved, the ribs seem not to be diagnostic and the pes is incomplete in the only known specimen of *Minmi*. A survey of the available relevant literature (Bohlin 1953, Brown 1908, Bunzel 1871, Coombs 1978, Eaton 1960, Gilmore 1930, Hulke 1881, Huxley 1867, Lull 1921, Maleyev 1952, Maryanska 1977, Moodie 1910, Nopsca 1928, 1929, Ostrom 1970, Owen 1884, Seeley 1879, 1881) reveals that while ankylosaur dorsal vertebrae are similar in form, there are character states that vary from genus to genus; these states are presented in Table 1.

One problem of the comparison of ankylosaurian dorsals is that the complete series of dorsals has been studied in only one form, *Ankylosaurus magniventris* (Coombs pers. comm.). There appears to be almost no progressive variation in the dorsals of that species, with the exception that the posterior intervertebral notch becomes increasingly shallow as one proceeds posteriorly in the series. For the type specimen of *Minmi paravertebra* the group of five vertebrae including the anterior end of the presacral rod must be the most posterior set of dorsals preserved, thus comparison of this group with the other six dorsals can suggest progressive variation. Such comparison suggests that the prezygapophyses become increasingly long posteriorly, and that the centra become increasingly broad. Thus for other taxa for which only dorsals of unknown position are described and figured these characters were not used.

In vertebral form *Minmi* agrees most closely with *Nodosaurus* (*sensu* Coombs 1978), from which it differs in that the diapophyses originate below the zygapophyses in *Nodosaurus textilis* (Lull 1921), but dorsal to them in *Minmi*. *Minmi* differs from *Hylaeosaurus* (*sensu* Coombs 1978) in having amphiplatyan dorsal centra, those of *Hylaeosaurus* being planoconcave (Hulke 1881), and in having relatively shorter prezygapophyseal processes. These processes of the dorsals of *Hylaeosaurus* extend anteriorly to the middle of the preceding centrum (Owen 1884). From *Sauropelta*, *Minmi* differs in lacking notocordal knobs, and having vertically orientated spines. From *Crataeomus* (see note to Table 1) *Minmi* differs in having amphiplatyan centra, in lacking the sulcus between the postzygapophyses described in that form (Seeley 1881), and in lacking the fossa anterodorsal to the parapophysis (Seeley 1881). Differences from other nodosaurids are given in Table 1. Ankylosaurids have neural canals less broad than in *Minmi*, and with the exception of *Talarurus*, parapophyses placed level with the top of the centrum, rather with the top of the neural canal.

Forms for which too little information is available for inclusion in Table 1 may also be distinguished from *Minmi*. *Acanthopholis* has bioconcave centra (Seeley 1879), and a neural canal much higher relative to the central height (Huxley 1867). *Stegosaurides* dorsals are represented by a centrum with a flat ventral surface (Bohlin 1953), quite unlike other known ankylosaur dorsal centra. That attributed to *Priconodon* (Lull 1911) tapers in dorsal view from anterior to posterior, also unlike other known ankylosaur dorsal centra. Dorsals of *Hoplitosaurus* are biconcave and described as having flattened sides (Gilmore 1914). None of these features are found in *Minmi*. *Saichania* (Maryanska 1977) and *Pinacosaurus* (Young 1935) have dorsal neural canals that are strongly compressed from side to side. This seems to be common in the dorsals of Asian Late Cretaceous ankylosaurs, as it is also true of *Talarurus* (Maleyev 1952, Fig. 7) and *Heishansaurus* (Bohlin 1953, Fig. 30b).

Thus *Minmi* can be distinguished from other ankylosaurs by its dorsal vertebral morphology, as well as by its possession of paravertebrae.

Table 1 suggests that *Minmi* agrees more closely with some nodosaurids (e.g. *Nodosaurus*) than with any ankylosaurid. Coombs (1978) gives no firm criterion applicable to the dorsal vertebrae for distinguishing nodosaurids from ankylosaurids. *Minmi* is thus classified as family *incertae sedis*, but may be a nodosaurid.

GEOGRAPHIC CONSIDERATIONS: *Minmi* is the first ankylosaur known from Australia, and one of the few reported from the Gondwana continents. The other reported forms are: *Loricosaurus scutatus* (von Huene 1929), known from armour and referred caudal vertebral centra (von Huene 1931) from north-central Argentina; *Lametasaurus indicus*, known from armour (Matley 1924), *Brachypodosaurus gravis*, known from a humerus (Chakravarti 1934), and undescribed material (Coombs 1978) from India; and undescribed nodosaurid material from Madagascar (Russell, Taquet and Thomas 1976). To this latter are possibly referable teeth described as *Stegosaurus madagascariensis* (Piveteau 1926) and recognised as ankylosaurian by Hoffstetter (1961). None of the described

TABLE 1: DORSAL VERTEBRAL CHARACTER STATES OF *MINMI* AND OTHER ANKYLOSAURS.

Genus	Central form	Notocordal knob	Keel	Neural spine	Neural canal	Transverse process	Parapophyses location	Fused ribs
*Crataeomus**	proc.	absent	absent	vert.	broad	slender	top of centrum	?
Hylaeosaurus	plan.	absent	present	?	narrow	?	top of canal	?
Nodosaurus	amph.	absent	absent	vert.	narrow	?	top of canal	present
Panoplosaurus	amph.	present	present**	post.	broad	broad	varies†	varies†
Sauropelta	amph.	present	absent	post.	broad	?	top of canal	?
Silvisaurus	amph.	absent	absent	post.	broad	broad	top of canal?	absent
Struthiosaurus	plan.	absent	present	post.	narrow	slender	top of canal	?
Minmi	amph.	absent	absent††	vert.	broad	slender	top of canal	present
Ankylosaurus‡	amph.	absent	absent	vert.	narrow	broad	top of centrum	present
Heishansaurus	amph.	absent	present	?	narrow	?	?	?
Talarurus	amph.	present	present	?	narrow	?	top of canal	present

* The genera here used follow Coombs 1978, and Maryanska 1977, with the exception of *Crataeomus*. This genus is treated as valid because of the different position of the pseudacromial process in *Crataeomus pawlowitschii* from that in *C. lepidophorus* (=*Struthiosaurus austriacus*) and *Struthiosaurus transylvanicus*. This difference is comparable to, but greater than, that between the scapulocoracoids of *Ankylosaurus* and *Euoplocephalus*.

** Keel present anteriorly on the centra only (Gilmore 1930).

† Variation between species not within a species.

†† Faint keel present on one of eleven centra.

‡ *Euoplocephalus* does not differ from *Ankylosaurus* in these states (Coombs, pers. comm.), and so this entry represents *Euoplocephalus* as well.

Abbreviations: proc. = procoelous; plan. = planoconcave; amph. = amphiplatyan; vert. = vertical; post. = posteriorly inclined.

forms are represented by material comparable to that of *Minmi*, so taxonomic relationships between them cannot presently be established.

The existence of an ankylosaur in Australia, in the Lower Cretaceous, underscores the widespread distribution of this group soon after its first appearance in the fossil record in the Neocomian (Coombs 1978). It also suggests the existence of a route into Australia during the early Cretaceous, or (accepting the existence of ankylosaurs during the Jurassic as postulated by Coombs 1978) the late Jurassic. Currently accepted dates for the separation of Australia from Antarctica are early Tertiary (Weissel and Hayes 1972, Deighton, Falvey and Taylor 1976), while the breakup of Gondwanaland is usually dated as Jurassic (e.g. Dietz and Holden 1970, Seyfert and Sirkin 1973): Rich (1975) in surveying the possible tetrapod dispersal routes across Antarctica into Australia concluded that any routes from South America would have been archipelagic after the mid-Mesozoic. The discovery of ceratodontid tooth-plates resembling those of *Neoceratodus forsteri*, the living Australian lung-fish, in the Upper Cretaceous Coli-Toro Formation of Argentina (Pascual and Bondesio 1976) suggests that such a route may have existed into the Upper Cretaceous. Molnar (1980) has presented evidence that such a route may have involved a filter, consonant with Rich's conclusion that the route would have been archipelagic.

Routes involving Africa or India are also possible, as these land masses were in connection with Antarctica into the Lower Cretaceous (Dietz and Holden 1970). Ankylosaurs are known from India and it seems that routes from Africa, at least, into the northern continents were open in the Lower Cretaceous (Molnar 1980, Sues and Taquet 1979). The presence of the freshwater plesiosaur *Leptocleidus* in the Lower Cretaceous of Queensland (Bartholomai 1966b), as well as in South Africa and western Europe, suggests that such a route could well have been taken by the ancestors of *Minmi*.

SUMMARY

A small Lower Cretaceous ankylosaur has been discovered in southeast Queensland. This is the first known ankylosaur from Australia. The ankylosaur, *Minmi paravertebra*, derives from the Minmi Mem. of the Bungil Fm. The existence of a presacral rod and fusion of one pair of ribs to the vertebra indicates that it is an ankylosaur. A set of peculiar elements of unknown function lie parallel to the dorsal neural spines, medial to the ribs. These elements, herein named paravertebrae, are preserved with the posterior three dorsals preserved. A fragment of one of the ribs shows a dorsal process just lateral to the tubercular process. *Minmi paravertebra* had a tetradactyl pes, and a ventral armour of small ossicles. Its dorsal vertebrae and ribs closely resemble those of other ankylosaurs.

The sequence of dorsal vertebrae of *Minmi* suggest that ankylosaur dorsals change slightly in form from anterior to posterior; the posterior vertebrae having longer prezygapophyses and broader centra than the anterior.

This specimen, although consisting of little more than the posterior portion of the trunk, minus pelvis, is still the most complete described from the southern hemisphere. It demonstrates that ankylosaurs were quite widespread soon after their first appearance (in the Neocomian) in the fossil record. They probably entered Australia via South America.

ACKNOWLEDGMENTS

Dr Alan Bartholomai brought this specimen to my attention, and kindly permitted the preparation and study of it. I am also grateful to Dr W.P. Coombs Jr, Mr G. Czechura, Dr R.W. Day and Dr M. Wade for their gracious assistance.

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PLATE 1.

FIG. A: The pes of *Minmi paravertebra* as preserved, in dorsal view. Bar represents 2 cm.

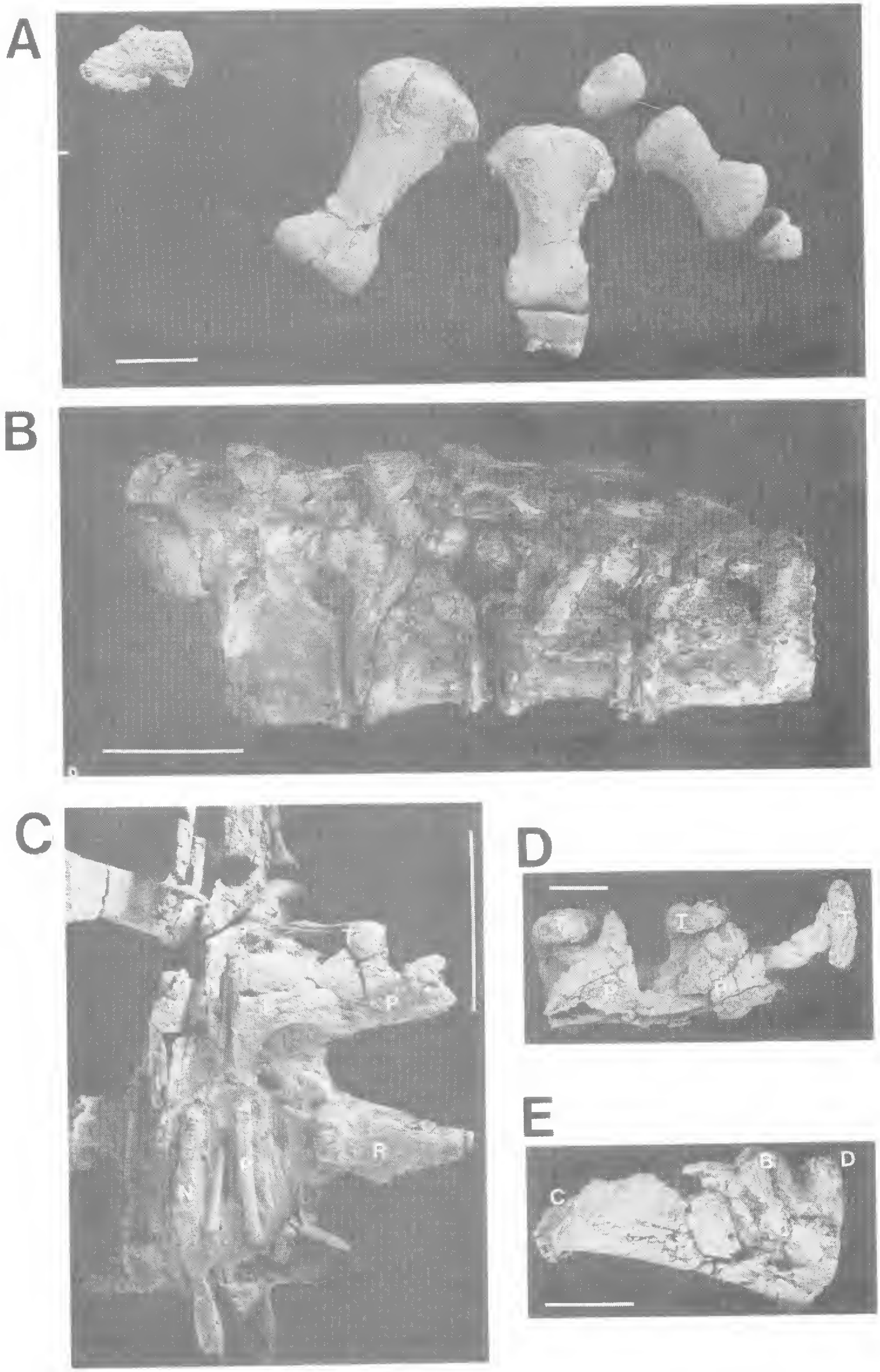
FIG. B: The last five dorsal vertebrae preserved, in left lateral aspect. The proximal portions of the ribs are still in place. Note the beginning of the presacral rod at right. Bar represents 5 cm.

FIG. C: The same, in dorsal aspect. Paravertebrae are visible on the right. Bar represents 5 cm.

FIG. D: Block of matrix with three transverse processes and two paravertebrae adherent. Anterior is to the left. Bar represents 2 cm.

FIG. E: Proximal portion of last left rib present, showing dorsal process just lateral to tubercular process. Bar represents 2 cm.

Abbreviations: B, tuberculum; C, capitulum; D, dorsal process; N, neural spine; P, paravertebra; R, rib; T, transverse process.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Mem. Qd Mus. **20**(1): 89–93, pl. 1 [1980]

A REVIEW OF THE DE VIS FOSSIL PIGEONS OF AUSTRALIA

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ABSTRACT

A review of Australian avian fossils *Nyroca effodiata* De Vis, *Leucosarcia proevisa* De Vis and *Lithophaps ulnaris* De Vis has shown that they cannot be distinguished from living species of pigeons, *Phaps histrionica* and *P. chalcoptera*. The type specimens of *N. effodiate* and *L. proevisa* are shown to be two parts of a single humerus.

From a large collection of fossil birds in the Queensland Museum, Charles W. De Vis described only three as extinct new species of pigeons: *Progura gallinacea* (1888); *Lithophaps ulnaris* (1891); and *Leucosarcia proevisa* (1905). *Progura gallinacea* was shown to be a megapode by van Tets (1974). While checking the De Vis material we found that the type of *Nyroca effodiata* (1905), described and named as a duck by De Vis is the distal part of the same humerus designated as the type of the pigeon *Leucosarcia proevisa* (Rich 1976, p. 59, fig. 4). We agree that this material is columbid but is not separable from modern species.

We have compared the type material of *Lithophaps ulnaris, Leucosarcia proevisa,* and *Nyroca effodiata* with every genus and almost all species of living Australian pigeons in the collections of the National Museum of Victoria (NMV), Melbourne; the Australian National Wildlife Collections, Division of Wildlife Research, CSIRO (ANWC), Canberra; and the Queensland Museum (QM). We have used the classification of Condon (1975) with amendments (*Emu* **76:** 216–7; **78:** 80–7).

SYSTEMATICS

'Leucosarcia proevisa' De Vis, 1905 and 'Nyroca effodiata' De Vis, 1905

TYPE SPECIMENS: *Leucosarcia proevisa*, QM F5511, proximal right humerus; *Nyroca effodiata*, QM F5544, distal right humerus; these two fragments fit together to form one nearly complete element lacking only part of the midshaft on the internal side (Plate 1). The combined specimen is now registered as QM F5511.

TYPE LOCALITY AND AGE: Wurdulumankula, eastern Lake Eyre Basin, South Australia, Quaternary (Fig. 1).

DIAGNOSIS

Differs from all other Australian pigeons except those in the genus *Phaps* by combining the following character states: head is highly domed, not flattened proximally as in *Petrophassa;* distinct ridge runs from external end of head across anconal surface of shaft diagonally to capital groove, which is absent in several pigeons including *Macropygia* and absent or only slightly indicated in *Ptilinopus;* long axis of ligamental furrow forms small acute angle with long axis of shaft, not large one as in *Ptilinopus, Petrophassa, Macropygia, Ducula, Leucosarcia, Geopelia, Chalcophaps* and *Ocyphaps;* proximal projection of long axis of shaft passes through external segment of head instead of lateral to it as it does in *Petrophassa;* internal surface of shaft just distal to pneumatic fossa deep, markedly planar, and delimited anconally by a sharp ridge that continues distally on the shaft crossing onto the anconal surface (extremely reminiscent of *Phaps histronica)* differing from most other Australian pigeons (including some *Phaps)* in which this area is more curved; internal margin of shaft not highly curved unlike that of *Petrophassa;* tubercle along

external border of shaft elevated further proximally from distal end (25% of total shaft length) than in other pigeon genera except *Phaps*, *Geopelia*, and *Columba;* distal end does not flare broadly unlike that in *Leucosarcia*, *Petrophassa*, *Columba* and *Ocyphaps;* ectepicondylar prominence is subdued, not protruding far laterally, unlike in *Petrophassa;* external condyle is deep relative to width i.e. distal end is not markedly palmoanconally compressed unlike in *Petrophassa*, some *Phaps* (not *P. histrionica)*, *Ptilinopus*, *Ducula*, and *Geopelia;* overall proportions of moderate length and indicate a gracile bird, not robust as in *Leucosarcia* or most *Columba*, and not as elongate as in *Ducula;* about the same size as some *Phaps*, *Columba*, and *Leucosarcia* (see Table 1), but smaller than *Lopholaimus*. Only the distal end of the humerous of *Lopholaimus* was available. It demonstrated no diagnostic qualitative differences, only differences in size.

COMMENT

When compared to every genus and most species of Australian pigeons, *'Leucosarcia proevisa'* clearly shares the greatest similarity with *Phaps*, the Bronzewings, and in fact should be included in that genus. The fossil exhibits no qualitative differences from any of the species of *Phaps*. *P. elegans* is distinctly smaller than the fossil, however. Both *P. histrionca* and *P. chalcoptera* are so similar in size and proportions to the fossil that precise assignment to either of these species seems impractical (see Table 1 and Fig. 2). Thus, *'Leucosarcia proevisa'* should be re-assigned to *Phaps* within the *P. histrionica/ chalcoptera* assemblage.

'Lithophaps ulnaris' De Vis, 1891

TYPE SPECIMEN: Complete right ulna, QM F1119 (Plate 1).

TYPE LOCALITY AND AGE: Darling Downs, South-eastern Queensland; Quaternary (Fig. 1).

FIG. 1: Localities of fossil pigeons in Australia and ranges of *Phaps chalcoptera* and *P. histrionica*.

TABLE 1: MEASUREMENTS (IN MM) OF HUMERI OF RECENT AND FOSSIL PIGEONS OF AUSTRALIA

Taxa	Total length of bird	Museum numbers, where applicable	N	Measurements A Total length	B Maximum Width proximal end	C Width of distal end	D Depth of external condyle
Ptilinopus cinctus	330	ANWC BS233	1	41·0	12·5	8·9	5·5
Ptilinopus superbus	230	ANWC BS244	1	30·8	11·1	7·7	4·6
Ptilinopus magnificus	430–560	ANWC BS255	1	46·0	15·9	11·5	6·7
Lopholaimus antarcticus	430	NMV B9229	1	—	—	13·6	8·4
Columba livia	330	NMV —	1	41·8	17·3	10·3	*c.*6·9
Streptopelia chinensis	280	NMV W6447	1	34·8	11·6	8·1	5·0
Macropygia amboinensis	400	NMV R6470	1	39·5	13·0	9·2	5·6
Geopelia cuneata	200	NMV W6185	1	19·4	6·8	4·9	2·8
Geopelia humeralis	290	NMV W4834	1	31·6	11·7	7·9	4·8
Chalcophaps indica	240	NMV W5915	1	32·3	11·1	8·8	4·8
Phaps chalcoptera	305	—	21	42·2–47·6	14·7–16·8	10·6–11·9	5·8–7·5
Phaps elegans	280	—	9	38·6–41·1	12·3–13·7	9·5–10·4	5·8–6·3
Phaps histrionica	280	—	4	44·2–45·3	14·9–16·8	9·9–10·7	6·7–7·3
Ocyphaps lophotes	320	NMV B8873	1	38·8	14·4	9·5	5·7
Petrophassa smithii	250	ANWC BS234	2	31·6–34·1	12·3	8·4– 8·9	5·1–5·6
Petrophassa albipennis	280	ANWC BS226	1	32·4	11·2	8·5	4·9
Petrophassa plumifera	200–230	NMV B8536	1	27·0	9·3	6·9	4·3
Leucosarcia melanoleuca	430	ANWC BS232	1	47·7	17·7	12·5	8·1
'*Leucosarcia proevisa* and *Nyroca effodiata*'	—	QM F5511/ F5544	1	45·5	>16·0	10·5	6·6

DIAGNOSIS

Tubercles on convex rear edge of fossil are of similar size and evenly spaced as in *Geopelia, Phaps, Petrophassa, Ocyphaps* and *Leucosarcia* and not with fourth turbercle from distal end being smaller than three more distal tubercles as in *Ptilinopus, Ducula, Lopholaimus, Chalcophaps, Columba* and *Streptopelia;* or with several median tubercles smaller than proximal and distal ones as in *Macropygia;* ulnae of *Geopelia* and *Petrophassa* are much smaller (see Table 2) and of *Leucosarcia* much larger and stouter; compared with species of *Phaps*, fossil decidedly longer than *P. elegans*, but comparable in size to *P. chalcoptera* and *P. histrionica*, neither of which exhibit significant differences in size and shape.

COMMENT

In overall morphology we can find no differences between *'Lithophaps'* and *Phaps*. *'Lithophaps ulnaris'* falls within the size range of both *Phaps chalcoptera* and *P. histrionica* (see Table 2 and Fig. 3), and we cannot distinguish between these two species. Thus, *'Lithophaps'* should be included within *Phaps* and *'L. ulnaris'* referred to the *P. chalcoptera/histrionica* assemblage.

TABLE 2: MEASUREMENTS (IN MM) OF ULNAE OF LIVING AND FOSSIL *PHAPS* PIGEONS IN AUSTRALIA

Taxa	n	Total length	Proximal width	Minimum shaft width	Distal width
Phaps chalcoptera	19	46·7 – 52·7	6·7 – 8·3	2·9 – 3·6	6·1 – 6·8
Phaps elegans	16	41·3 – 44·3	5·9 – 6·9	2·6 – 3·0	5·2 – 5·6
Phaps histrionica	3	50·4 – 52·5	5·8 – 8·0	3·0 – 3·2	6·1 – 6·5
'Lithophaps ulnaris'	1	>47·3	6·7	2·9	5·1

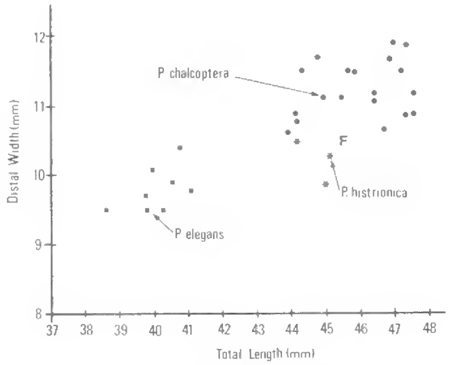

FIG. 2: Plot of humeral measurements of extant species of Australian *Phaps* and F, the fossil *'Leucosarcia proevisa* and *Nyroca effodiata'*, QM F5511/F5544.

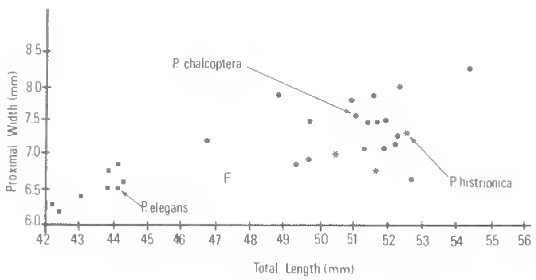

FIG. 3: Plot of ulnar measurements of extant species of Australian *Phaps* and F, the fossil *'Lithophaps ulnaris'*, QM F1119.

CONCLUSIONS

A review of the fossil pigeon material described by C.W. De Vis has demonstrated that *'Leucosarcia proevisa'*, *'Nyroca effodiata'* and *'Lithophaps unlnaris'* should be included within the living genus *Phaps*, the Bronzewings. Although the fossils represent birds distinctly larger than the Brush Bronzewing *(P. elegans)*, they fall within the range of variability exhibited by both the common Bronzewing (*P. chalcoptera*) and the Flock Pigeon (*P. histrionica*), and we can see no decisive method for distinguishing these species on the basis of the humerus or the ulna. We can thus assign the fossils only to the *chalcoptera/histrionica* assemblage. Although somewhat south or southeast of the modern geographic range of *P. histrionica*, the fossil occurrences in northern South Australia and southeastern Queensland are within the range of the currently widespread *P. chalcoptera*.

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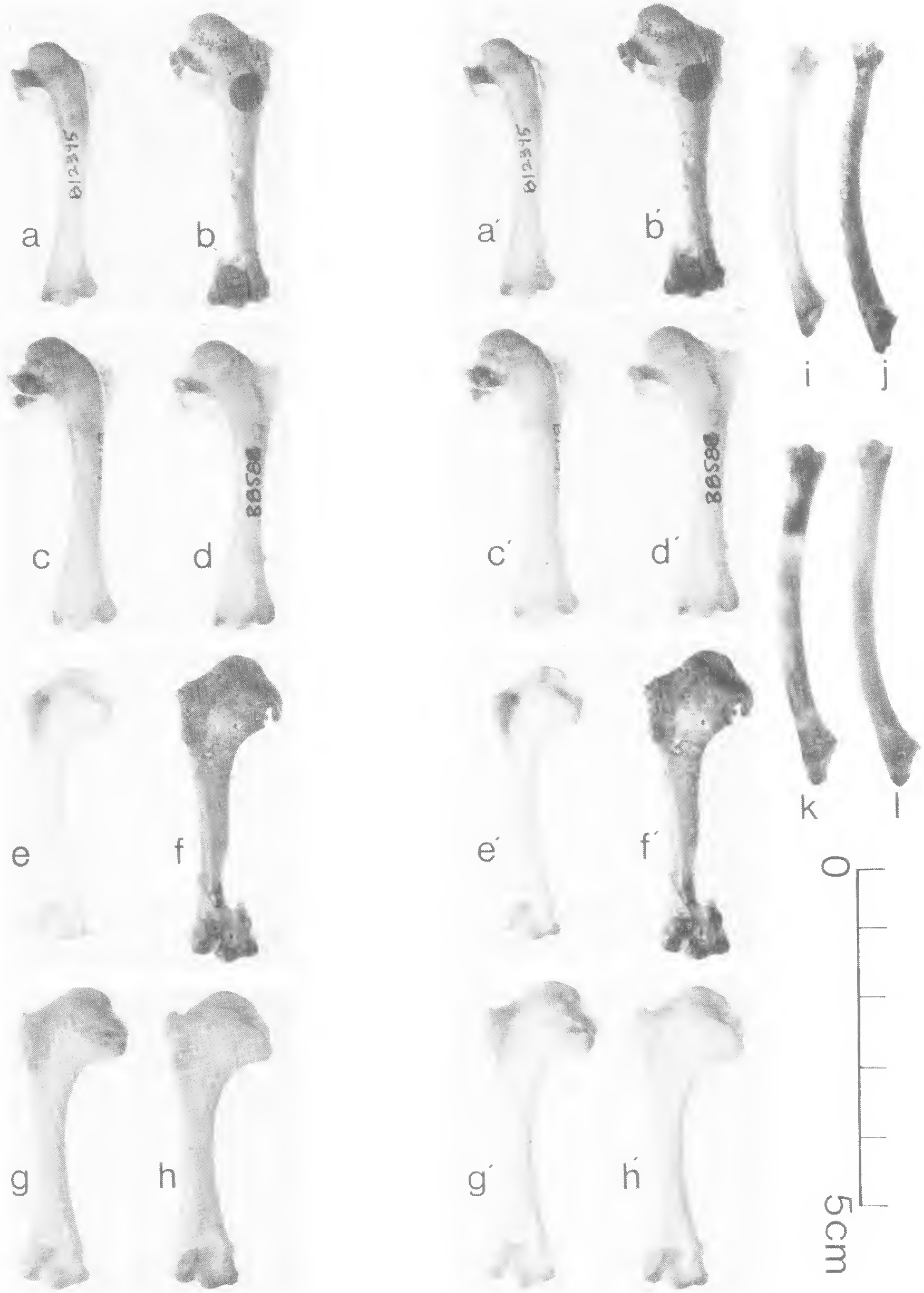
PLATE 1

Humeri and ulnae of fossil and recent pigeons. Right humeri, anconal views, stereo pairs: a, a' *Phaps elegans* (NMV B12395); b, b' *'Leucosarcia proevisa* and *Nyroca effodiata'*, QM F5511/F5544); c, c' *Phaps chalcoptera* (NMV B12400); d, d' *Phaps histrionica* (NMV B8588). Right humeri, palmar views, stereo pairs: e, e' see a; f, f' *Lithophaps Ulnaris, Ulnaris QM–1119* g, g' see c; h, h' see d. Right ulnae lateral views: i, see a; j, see b; k, see c; and l see d.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Mem. Qd Mus. **20**(1): 95–101, pl. 1 [1980].

TWO NEW SPECIES OF SKINKS FROM MID-EASTERN QUEENSLAND RAINFOREST

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ABSTRACT

Two species of skinks *(Sphenomorphus luteilateralis, Sphenomorphus amplus* spp. nov.) are described from restricted rainforest habitats in mid-eastern Queensland. The former is confined to high altitude, mixed notophyll vine forest in the Eungella National Park, near Mackay. *Sphenomorphus amplus* occurs at lower altitudes, usually associated with rocks along creeks, in simple and complex notophyll vine forest in the Eungella National Park, and in complex notophyll vine forest in the Conway State Forest, near Proserpine.

Until recently the reptiles of mid-eastern Queensland had not been surveyed methodically. Surveys by the Queensland National Parks and Wildlife Service commenced in the area in 1975 and, in that year, the Australian and Queensland Museums, supported financially by the Australian Biological Resources Study, undertook fauna surveys in the area. Twelve sites representative of the different rainforest structural types and floristic provinces of mid-eastern Queensland were examined. Eight sites were surveyed from Mackay to Proserpine, an area that was virtually unknown herpetologically. Preliminary results of surveys by the Australian and Queensland Museums have been presented (Broadbent and Clark 1976, Queensland Museum 1976, Covacevich 1977). As expected, many undescribed species of frogs and reptiles were collected, particularly in the Eungella National Park sites near Mackay. Amongst the undescribed material are two large, lygosomine skinks.

Genera of the sub-family Lygosominae, to which *Sphenomorphus* Fitzinger 1843 belongs, have been defined and their relationships discussed by several authorities: Gray (1845), Boulenger (1887), Smith (1937), Mittleman (1952), and Greer (1970). Greer (1970, p.171) has noted . . . 'the greatest single taxonomic problem with the lygosominae is the delineation of genera' . . . Within this subfamily the genus *Sphenomorphus* presents special problems of delineation. Skinks currently assigned broadly to *Sphenomorphus* occur widely in tropical Africa, southern Asia, Australia, New Zealand (Storr, 1967), and New Guinea (Scott, Parker, and Menzies 1977). Storr (1967) and Cogger (1975) have recently defined this genus for Australia to include about 20 species, all of which lack supranasal scales. A New Guinea genus, *Otosaurus,* was erected by Gray (1845, p.93) for specimens which differed from *'Sphenomorphus'* essentially in having 'super nasal 2, contiguous'. This genus was maintained by both Smith (1937, p.218) and Mittleman (1952, pp.6–7), whose work maintaining *Otosaurus* for species with supranasals (e.g. *O. cumingi,* from New Guinea and Southeast Asia) is the most recent 'total' discussion of all lygosomine genera and their broad relationships. The species with supranasal scales have, however, been referred to *Sphenomorphus* by Loveridge (1948), Greer (1970), and Scott, Parker, and Menzies (1977) without discussion.

The first species *(S. luteilateralis* sp. nov.) is easily referred to *Sphenomorphus* as it is defined for Australian species by Storr (1967) and Cogger (1975). It is apparently related to members of the *S. murrayi* group within *Sphenomorphus* — *S. murrayi* (Boulenger), *S. tenuis* (Gray), *S. tigrinum* (De Vis). All share the following features in addition to those described for *Sphenomorphus* — large size, robust form, and ground-dwelling habits.

The generic placement of the second species (*S. amplus* sp. nov.) is more difficult to decide upon, because it has distinct supranasal scales, a feature which would exclude it from *Sphenomorphus* as it has been defined by Storr (1967) and Cogger (1975) for Australian species, and from *Sphenomorphus* as it is defined fully by Mittleman (1952). In this case *S. amplus* sp. nov. would most appropriately be assigned to *Otosaurus*. However, considering the current lack of understanding of lygosomine generic boundaries and relationships generally, and the status of *Sphenomorphus* species 'groups' in particular, and noting that recent authorities have 'lumped' *Otosaurus* in *Sphenomorphus*, it seems reasonable to place *amplus* in *Sphenomorphus* while recognising its affinity with species of the *Otosaurus* group within *Sphenomorphus* from New Guinea.

Sphenomorphus luteilateralis sp. nov.
(Plate 1,a)

Material Examined

Holotype: QM J31685 Eungella National Park 148° 35'E, 21° 03'S coll. K.R. McDonald, D. Vlasak,9.i.1976, closed forest.

Paratypes: J31674–J31684, J31686, same locality and data as holotype; J31687–8, 15.iii.1975, Eungella National Park, as for holotype, col. K.R. McDonald, J. James; J31689, 14.iii.1975, same data as for J31687; J31690, data as for holytype; J31691–7, new born young of three females, same data as holotype; AM R47765–70, 14.iv.1975, Eungella National Park, Dalrymple Heights, coll. P. Webber; R47763–4, 14.iv.1975, Eungella National Park, coll. H. Posamentier; R47855–6, 3.iv.1975. Eungella National Park near Vlasak property, coll. P. Webber; R47941–3, 6.v.1975, Mt William, Eungella National Park, coll. P. Webber; R47497, 21–26.iv.1975, Mt William, Eungella National Park, coll. P. Webber.

Diagnosis

S. luteilateralis most closely resembles the southeastern Queensland/northeastern New South Wales skink *S. murrayi* (Boulenger 1887). It may be distinguished from *S. murrayi* as follows: prominent orange coloured sides with white occellations, distinct dark patch above fore limb; 37–41 mid-body scales *vs* 29–33 in *S. murrayi*.

Description of Holotype

Snout-vent length 87 mm; tail regenerated. Habit stout. Tip of snout–forelimb/axilla–groin = 33/46 mm. Snout short, obtuse. Rostral broad, forming a suture with the nasals and frontonasal. Frontonasal slightly broader than long, bordered posteriorly by two large prefrontals which just touch. Frontal about 2·5 times as long as broad, and narrow posteriorly; about as long as the frontoparietals and interparietal together. Frontal in contact with first and second supraocular. Supraoculars four, the second largest and the fourth smallest. Supraciliaries 7. Frontoparietals and interparietal distinct, the frontoparietals slightly larger. Supralabials 6, the fifth contacting the eye and immediately below the eye centre. Ear opening large, oval (about the same size as eye) with a deeply set tympanum. No auricular lobules. Mid-body scales 37. Mid-dorsal scales slightly larger than lateral and mid-ventral scales. Two enlarged preanals. Limbs and digits moderately long. Twenty-two lamellae under fourth toe. Colour: In preservative, basically brown dorsally with a few scales with darker markings. A conspicuous large black patch occurs above the forelimb with a small dark area on the dorsal edge of ear and another dark mark exists dorsolaterally between ear and forelimb patches. Ventrally white. Labials and chin shields white. Laterally, between head and forelimb, scales off-white; between forelimb and hindlimb faded orange with distinct white occellations. Limbs are basically similar in colour to the dorsal surface but they have more dark scales. In life the dorsal surface is darker brown and the faded orange is a bright burnt-orange.

Variation in Paratypes

SVL 52–92 mm. Tail 77–112 (only 5 specimens have original tails and most of these are juveniles). The following variation from the holotype description has been observed in the paratypes.

Frontonasal scale: J31682 has a fragmented scale.

Colour: Differences are minor. Juveniles are similar to adults except that the orange lateral sides are not as intensely coloured. In some specimens the dark patches near the forelimb are not as intensely coloured as in the type.

Mid-body scales: Counts in 38 paratypes vary from 36–41 as follows — 36 (2 specimens, 5·5%), 37 (6, 15·5%), 38 (17, 44·5%), 39 (9, 23·5%), 40 (2, 4·5%), 41 (2, 5·5%). No mid-body count could be taken from one damaged juvenile specimen.

Lamellae: Counts under the fourth toe vary from 17–22 as follows in 39 paratypes 17 (1, 2·5%), 18 (5, 13%), 19 (9, 23·5%), 20 (11, 28%), 21 (7, 18·5%), 22 (6, 15·5%).

Supraciliaries: These vary from 6–8 as follows 6 (2, 5%), 7 (34, 87%), 8 (3, 8%).

Supraoculars: These vary only slightly with one having 3 and two having 4 supraoculars on one side and three on the other.

Prefrontals: These meet (10 specimens) or are separated (29 specimens).

Distribution and Habitat

Sphenomorphus luteilateralis is known only from the Eungella National Park on the slopes of Mount William. All specimens were collected in mixed notophyll vine forest above 900 metres.

S. luteilateralis is a common species where it occurs. Eighteen specimens were seen in 1½ hours in about 2 ha of rainforest.

Notes

Specimens of *S. luteilateralis* were observed 'sunning' on palm trunks and fronds on the forest floor as well as on dead logs and were also found in rotting logs and palm frond bases. They forage in leaf litter, are always found on the ground, and show no tendency to climb when disturbed.

Females bear five individuals viviparously. SVL and tail lengths of 15 individuals at birth varied between 29·0–32·7 (mean 30·64, SD 1·31) and 38·6–45·3 (mean 41·60, SD 3·53).

S. murrayi and *S. luteilateralis* are similar in external morphology as well as habitat preferences and habits. Both species usually bear 5 live young, are found in rainforest at higher elevations, are crepuscular in habit, and are found in similar niches. Both are terrestrial and live in decaying logs and forest floor vegetation. Further, both species are strongly territorial. Single pairs (♂, ♀) of both species live harmoniously in captivity but, where more specimens are kept in the one cage, fighting occurs constantly. Warnings are given to intruders of territory by vigorous waving of the tail in the leaf litter. The defendant of the territory invariably faces the intruder when making these aggressive warnings. Fighting sometimes eventuates, usually in the form of biting around the head until one specimen retreats. Juveniles are not attacked and are tolerated in the adult territory. This pattern has also been observed in the field.

S. murrayi and *S. luteilateralis* are, however, widely separated geographically. *S. murrayi* is known from above 150 m from northeastern New South Wales and southeastern Queensland (as far north as the Conondale Range) while *S luteilateralis* is confined to the high altitude slopes (above 900 metres), of Mt William, mid-eastern Queensland.

Sphenomorphus amplus sp. nov.
(Plate 1, b)

Material Examined

Holotype: QM J26054, Finch Hatton Creek, Eungella National Park, ME.Q., coll. K.R. McDonald, 7.ii.1975.

Paratypes: QM J31647, 10.i.1976, Eungella Hotel Grounds, coll. K.R. McDonald, P. Wilson; J31648, 14.i.1976, Broken River, Eungella National Park, coll. K.R. McDonald, J. Miller; J31649, 7.i.1976, Wishing Pool, Eungella National Park, coll. V.R.J. Hansen, K.R. McDonald; J31650 – 2, 15.i.1976, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen, K.R. McDonald; J31653, 2.ix.1975, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen; J31654, 13.ix.1975, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen; J31655, 15.i.1976, Finch Hatton Gorge, Eungella National Park, coll. K.R. McDonald, V.R.J. Hansen; J31656, 17.iii.1975, Finch Hatton Gorge, Eungella National Park, coll. K.R. McDonald, J. James; J31657, 25.iii.1975, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen; J31658, 17.ii.1975, Finch Hatton Gorge, Eungella National Park. coll. K.R. McDonald, V.R.J. Hansen; J31659, 15.i.1976, Finch Hatton Gorge, Eungella National Park, coll. K.R. McDonald, V.R.J. Hansen; J31660 21.vii.1975, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen; J31661 – 73, 5.i.1976, Finch Hatton Gorge, Eungella National Park, coll. K.R. McDonald, V.R.J. Hansen; J32784–5, 19–22.iv.1975, Brandy Creek, Conway State Forest, coll. J. Covacevich, R. Monroe, P. Filewood; J33980, J33983, 7–14.iv.1975, Finch Hatton Gorge, Eungella National Park, coll. R. Monroe, J. Covacevich, P. Filewood; J33984, 8.iv.1975, Finch Hatton Gorge, Eungella National Park, coll. V.R.J. Hansen; J33985, J34022 –3, J34026–9, J34034–5, J34061, J34084, 7–14.iv.1975, Finch Hatton Gorge, Eungella National Park, coll. J. Covacevich, R. Monroe, P. Filewood; AM R61483, R61482 (formerly J33981–2), 7–14.iv.1975, Finch Hatton Gorge, Eungella National Park, coll. J. Covacevich, R. Monroe, P. Filewood.

Diagnosis

S. amplus most closely resembles the Irian Jaya (Western New Guinea) species *Otosaurus mimikanus* (Boulenger 1914). It may be distinguished from *O. mimikanus* as follows — supranasal scales (usually 2 pairs* *vs* one pair); mid-body scale count (41–52 *vs* 40); lamellae under fourth toe (22–26 *vs* 15); colour and pattern

* See discussion of variation in the paratypes

(see type description Boulenger, 1914). These features also readily distinguish *S. amplus* from all Australian species of *Sphenomorphus*. No other Australian *Sphenomorphus* species have supranasals and only one species group has more than 40 mid-body scales. Species of the *S. quoyi* group have 24–44 mid-body scales (Cogger, 1975) but in addition to lacking supranasals, these species are strikingly coloured olive-brown dorsally with prominent yellow-cream dorsolateral longitudinal stripes, a pattern which is never present in *S. amplus*.

Description of Holotype

SVL 100 mm; tail (original) 143; head width 15·2. Habit stout. Tip of snout–forelimb/axilla–groin = 40/48 mm. Snout short, obtuse. Rostral broad, forming a suture with the single nasal and the anterior supranasal. Two supranasals; on each side the anterior ones form a median suture. Frontonasal approximately equally broad as long, bordered posteriorly by the large prefrontals which form a median suture. Frontal about three times as long as broad and narrow posteriorly; about as long as the frontoparietals and the interparietal together. Frontal in contact with the first and second supraocular. Supraoculars 5, the anterior one largest and posterior one smallest. Supraciliaries 9. Frontoparietals and parietal distinct and about equal in size. Supralabials 7; fourth, fifth, and sixth under the eye. Ear opening large, oval about the same size as the eye, and with deeply set tympanum; no auricular lobules. Mid-body scales 46. Mid-dorsal scales about twice as large as mid-ventral and lateral scales. Two enlarged preanals. Limbs and digits moderately long; lamellae under fourth toe 23.

Colour: In preservative, grey-brown dorsally and cream ventrally, with a conspicuous black patch above the forelimb. Labials and chin shields blue-grey, edged with narrow dark brown-black lines which are broader on the labials, giving the appearance of irregular blotching. Laterally, between the head and the forelimb, scales are also basically blue-grey. These have small dark spots which form a series of regular narrow lines. Dorsally between the neck and tail there is a series of irregular transverse light brown bands. Limbs also irregularly banded with light brown. On the tail the light bands are more numerous and regular. Colour pattern in life was basically similar but some colours were stronger e.g. olive-brown *vs* grey-brown dorsally; lemon *vs* cream.

Variation in Paratypes

SVL 40–115 mm. Tail 78–126 mm (only 12 specimens have original tails and most of these are juveniles). The following variation from the holotype description has been observed.

Supranasal scales: In three specimens (J31666, J31664, J34023) there are two supranasals on each side. The anterior pair do not form a medium suture. One specimen (J31660) has two supranasals on one side and a single, large supranasal on the other. They form a median suture. In J34027 the supranasals are as in J31660 but they do not form a median suture. J31652 has only one large supranasal on both sides (presumably representing fused smaller scales) which form a median suture. In three juvenile specimens (J34026, J34061, J33984) the posterior supranasals fuse with the loreals. The anterior supranasals in all three specimens form median sutures.

Frontonasal scale: J32785 (a juvenile) has fragmented frontonasal and right prefrontal scales.

Colour: Differences are minor. Shading of basic colouring is more intense in some specimens and the head scales in juveniles are sharply lined in black.

Mid-body scales: Counts in the 45 paratypes vary from 41–52 as follows. 41 (4 specimens, 9%); 42 (6, 13·5%); 43 (5, 11%); 44 (10, 22%); 45 (6, 13·5%); 46 (8, 18%); 48 (3, 7%); 51 (1, 2%); 52 (2, 4%).

Toe lamellae: Counts under the fourth toe vary from 22–26 as follows — 22 (7, 16%); 23 (21, 47%); 24 (11, 24%); 25 (5, 11%); 26 (1, 2%).

Supraciliaries: These vary from 8–10 as follows — 8 (11, 24%); 9 (23, 52%); 10 (11, 24%).

Supraoculars: There is only slight variation — 5 (42 specimens) or 6 (3).

Distribution and Habitat

S. amplus is known from only two areas in mid-eastern Queensland — Eungella National Park, west of Mackay and Conway State Forest, east of Proserpine. It is confined to closed forest. In the Eungella National Park it occurs between 300 and 900 m usually amongst and near granite outcrops near streams. It is a common element of the reptile fauna of this reserve. *S. amplus* is apparently less common in the Conway State Forest closed forests. Here it frequents buttresses and roots of large trees, especially *Ficus* sp. and rocks near creeks. It has not been found with *S. luteilateralis* which occurs in the same area but which is apparently confined to higher altitudes.

NOTES

Sphenomorphus amplus is an unusual species. In the Eungella National Park specimens were frequently observed at night sleeping on open rock faces, apparently for warmth. When handled or fighting they emit a sharp, loud 'squeaking' sound. The former feature has not been reported for any other Australian skinks and the latter is apparently an unusual feature amongst Australian skinks. It has been reported in some *Tiliqua* and in two other Australian species (Greer 1976) — *Sphenomorphus murrayi, Tropidophorus queenslandiae.*

S. amplus and *S. tenuis* are sympatric in the Eungella National Park and are often found very close together, but apparently occupy different niches. *S. amplus* is invariably found on or very near rocks in moist areas, usually near creeks. *S. tenuis*, by comparison, favours rotting logs and the bases of large trees, especially those with hollows and crevices. *S. amplus* is viviparous. A gravid female (J31652) carried five well developed young along with an undeveloped egg in the oviducts.

The external morphological affinities of *S. amplus* lie with Southeast Asian and New Guinea species referred to *Otosaurus* (incorporating *Parotosaurus*) as listed by De Rooij (1915) and Smith (1937), but referred to *Sphenomorphus* by Loveridge (1948), Greer (1970), and Scott, Parker, and Menzies (1977). *O. mimikanus*, is described and well illustrated by Boulenger (1914). It shares the following features with *S. amplus* — large, robust form; high mid-body scale count; supranasals; colour pattern (see diagnosis for differences). Whether these similarities indicate a real relationship of this species (which is confined to mid-eastern Queensland) to Asian and New Guinea species, or whether they are purely superficial, remains to be determined. This question highlights current unresolved problems in the relationships between lygosomine skinks of the Australian region, particularly those currently referred broadly to *Sphenomorphus*.

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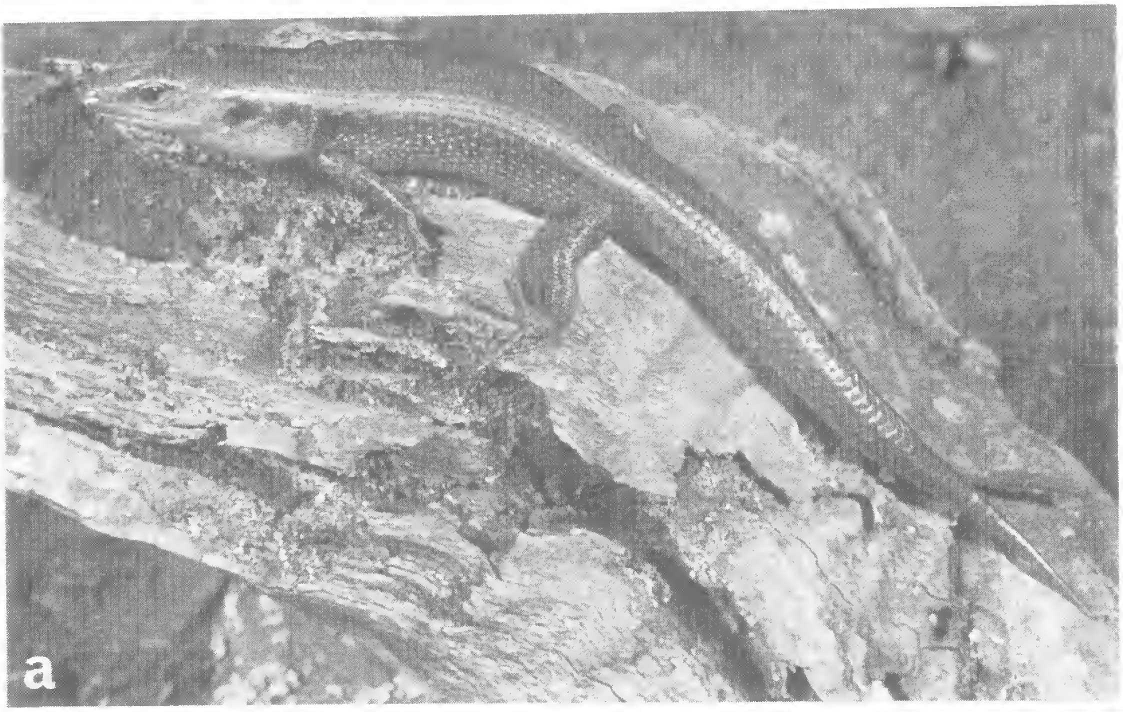
PLATE 1

a. *Sphenomorphus luteilateralis* sp. nov., Mt William, Eungella National Park, via Mackay.

b. *Sphenomorphus amplus* sp. nov., Finch Hatton Gorge, Eungella National Park, via Mackay.



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THE EMERALD MONITOR *VARANUS PRASINUS* (SCHLEGEL): AN ADDITION TO THE AUSTRALIAN MAINLAND HERPETOFAUNA

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ABSTRACT

The occurrence of the Emerald Monitor *Varanus prasinus* (Schlegel) on the Australian mainland, is confirmed by the collection of three specimens from the McIlwraith Range area, Cape York Peninsula. These specimens are compared with the four currently recognized subspecies of this monitor and assigned tentatively to the nominate race. Difficulties encountered in the definition of these subspecies are briefly outlined.

The Emerald Monitor (*Varanus prasinus*) is widely distributed throughout mainland Papua New Guinea, West Irian and adjacent island groups. This monitor may be distinguished from other *Varanus* species by the combination of the following features; round nostril, slightly compressed tail which lacks a median double keel, and the presence of transverse supraoculars (Cogger 1975; De Rooij 1915; Mertens 1942, 1959). Mertens (1959), in the most recent treatment of Indo-Australian *Varanus* species, recognises four subspecies of *V. prasinus*, all from New Guinea and adjacent islands:

1. *Varanus prasinus prasinus* (Schlegel): mainland New Guinea, Misol, Salawatti, Goodenough, 'islands of Torres Strait' and the d'Entrecasteaux Archipelago.
2. *Varanus prasinus beccarii* (Doria): Aru Islands, and possibly from Fak Fak (West Irian).
3. *Varanus prasinus bogerti* Mertens: the d'Entrecasteaux Archipelago.
4. *Varanus prasinus kordensis* (A.B. Meyer): Biak, northwest New Guinea.

Australian records of *V. p. prasinus* (from the Torres Strait only) are based on Gunther (1877, 1879) and Boulenger (1885) who record *Varanus prasinus* as occurring on islands of Torres Strait, Cornwallis (=Dauan), and Murray Islands. Cogger (1975) notes unconfirmed reports of this monitor from northern Cape York Peninsula but, until now, there have been no specimen records of *Varanus prasinus* from mainland Australia.

In August 1978, an unusual dark specimen of *Varanus* was collected by the author at Buthen Buthen, east of Coen, far northern Queensland. Subsequently, two additional similar specimens were collected in the same area by officers of the National Parks and Wildlife Service. Examination of these specimens confirms the presence of *V. prasinus* on the Australian mainland.

MATERIALS AND METHODS

The three Cape York Peninsula specimens were compared with specimens of *V. prasinus* in the Queensland Museum (QM) and Australian Museum (AM) collections. In addition, the type of *Varanus prasinus bogerti* in the American Museum of Natural History (AMNH 41639), was also examined and compared with these specimens.

The following measurements were recorded in millimeters; snout–vent length (SVL), tail length (TL), head length (HL), head depth (HD), head width (HW), eye–naris distance (EN), internarial distance (IN), and snout to anterior edge of naris (SN). The values are expressed by the mean value followed by the range in parentheses.

The term 'New Guinea' used below refers to the whole island exclusive of political subdivisions.

Description of Australian Mainland Secimens of *Varanus prasinus*

SVL 237·6 (214–250); TL 479·6 (425–524); HL 42·0 (36·0–49·7); HD 20·6 (16·2–23·9); HW 23·7 (19·2–26·7); EN 13·5 (12·6–14·2); IN 8·3 (7·4–8·8); SN 10·2 (9·5–11·2).

Head long and narrow, about twice as long as broad and 1·7 times as long as high. Snout rounded in profile. Canthus rostralis indistinct, rounded and slightly elevated above the nostril which is closer to tip of snout than eye. Nostril rounded, inclined posteriorly in lateral aspect and visable from above (see Plate 1). Ear opening large, oval and more or less vertically orientated.

Dorsal head scales variable in size and shape, largest between snout and interorbital region (Plate 1). Individual scales well demarcated by deep suture lines, not forming a continuous layer. Individual scales may be pitted, weakly tuberculate or smooth, with structures demarcated by black pigmentation. A series of about five transversely enlarged supraoculars, some or most of which may be divided. Occipital scales similar, but smaller in size and less smooth. 35–36 scales around head from rictus to rictus. Temporal scales, smaller than the dorsal head scales; individual temporal scales subequal, and elliptical in shape, forming oblique rows (Plate 1). Nuchal scales transversely enlarged, rounded in profile. Neck scales becoming longer than wide posteriorly. Low keels present on last third of neck. All neck scales rounded in profile.

Anterior chin shields little differentiated except for enlarged pair immediately posterior to mental. Mental groove weak. Dorsal body scales longitudinally keeled, rectangular or slightly rounded in profile; in 90–99 scale rows at midbody. Lateral scales subequal. Ventral scales with apical pits, in 86–89 rows from gular fold to hindlimb insertion. Limbs well developed with strong claws. Palms and soles black. Approximately 35–38 smooth lamellae under 4th toe, (except for 6–10 distal lamellae) divided and gradually merging with the similarly shaped scales of sole. Caudal scales keeled, subequal, and in regular annuli to tail tip. Proximal caudal scales with apical pits, each being replaced distally by a short spine. Plate 1 shows QM J31566 in dorsal view.

Colouration: All three specimens are predominantly black dorsally and laterally on both body and limbs. The area from the tip of snout to the interorbital area is light bluish green, with black suture lines (except on snout itself). A short yellowish bar is present above the ear opening and may extend forward towards the posterior corner of the eye. Individual body scales may have tiny yellowish spots, which when viewed from a distance, combine to form indistinct chevrons across the body. These indistinct chevrons are separated by narrow areas of black. These spots are more noticeable after preservation than in life. Yellowish colour is more noticeable on the tail where thin bands are present in middle of each annuli. Ventral surface of body and limbs pale yellowish-green.

Comparison with Recognized Subspecies

Using Mertens (1942, 1952) data, these specimens may be distinguished from *V. p. beccarii* (Doria) and *V. p. kordensis* (A.B. Meyer) by respective colouration differences (dark dorsum/light venter vs dark dorsum and venter vs green and black network pattern on dorsum/light venter). The Cape York specimens also lack the prominent neck keels and narrow, pointed snouts of these two subspecies. Comparison with the type of *V. p. bogerti* Mertens (AMNH 41369) shows that the three Australian specimens differ from this subspecies on the basis of more rounded snouts, larger dorsal head scales, weakly keeled neck scales and possession of a regular, oblique series of temporal scales.

Separation from the nominate race, *V. p. prasinus* (Schlegel), is difficult. Only two consistent differences were apparent when comparing New Guinea *V. p. prasinus* with the Cape York specimens. These differences being the black (as opposed to green) dorsal colouration and the more prominent body keels of the Australian specimens. Ventral scale counts overlap (New Guinea; 71–86, N=9: Cape York; 86–89, N=3), while midbody scale counts for Cape York Peninsula specimens (90–99: N=3) fall within the range of variation of New Guinea material (74–105: N=9). Minor differences were detected with respect to the degree of 'pitting' on head scales, depth of dorsal head scale sutures and the appearance of nuchal and neck scales. However, as New Guinea *V. p. prasinus* showed variation among themselves in regard to these features, their diagnostic value was considered questionable.

Field Observations

The Buthen Buthen specimen (QM J31566) was collected in semi-deciduous mesophyll vine forest (altitude 60–100 m). It was discovered climbing through the crowns of secondary story vegetation, which formed a more or less continuous layer three to four meters above ground level. The Leo Creek Road specimen (QM J35450) was collected from the outer surface of

the tree canopy in deciduous vine thicket (altitude 280–300 m). It was estimated to be some fifteen meters above ground level (J. Winter, pers. comm.). The specimen from Lankelly Creek (QM J35451), was collected in *Eucalyptus*-dominated open forest within 50 meters of deciduous vine thicket (altitude 520–540 m). It was first seen on the ground, then collected from a standing eucalypt (J. Winter, pers. comm.).

Mertens (1942, 1950) notes that the tail tip in both *V. p. prasinus* and *V. p. bogerti* is 'somewhat prehensile'. The prehensile nature of the tail tip of QM J31566 was readily apparent before collection and prior to preservation. In addition to the prehensile tail-tip, climbing in these monitors appears to be facilitated by the structure of the surface tissue on the soles of fore and hind feet. These surfaces are covered by soft black tissue, which feels sticky on contact and appears to give additional support to the climbing animal. An investigation of the structure of this tissue is in progress.

The localities from where the species were collected are shown in Fig. 1.

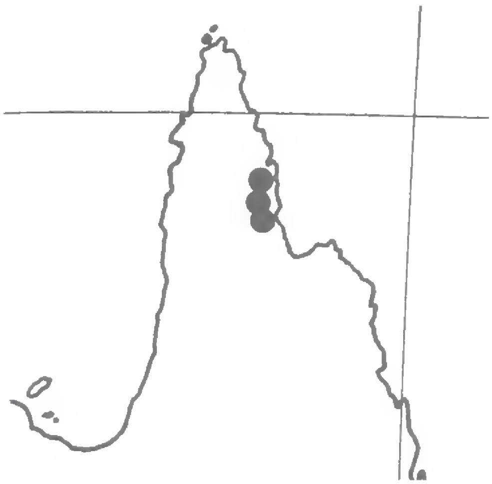

FIG. 1: Distribution of *Varanus prasinus* in Queensland.

DISCUSSION

Although Cape York Peninsula specimens are distinct from *V. p. prasinus* in colour and body keels, there are no apparent consistent differences in the structure and shape of head scales and the condition of the nuchal and neck scales. In the absence of convincing evidence to the contrary, it is felt that the Cape York population should be tentatively assigned to the nominate race of this monitor *(Varanus prasinus prasinus)*.

Two considerations have largely influenced this decision. The first involves the rather confused taxonomy of *prasinus* subspecies. Mertens (1959), while recognizing the four subspecies, drew attention to the existence of a number of problematical populations of this monitor; *kordensis*-like individuals from the mainland and small island groups; *beccarii*-like individuals from the south-west mainland of New Guinea; and a *bogerti* 'relative' from the d'Entrecasteau group. A specimen (QM J1190) apparently collected from Rossel Island (Louisiade Archipelago) presents a further complication. *V. prasinus* has not previously been reported from this island group, and this specimen was not examined by Mertens. It is not possible to satisfactorily assign it to any existing subspecies using available literature or specimens.

The second consideration concerns the apparent trend of *V. prasinus* to become increasingly melanistic in outlying populations. The greatest degree of melanism is found in the insular forms *V. p. bogerti* and *V. p. beccarii,* a lesser degree in the *'kordensis'* pattern and the least in predominantly green *V. p. prasinus*. Cape York specimens appear intermediate between the fully melanistic and *'kordensis'* forms. Until a suitable series of this monitor from southern New Guinea, Torres Strait and northern Cape York Peninsula is available for investigation, the possibility of clinical variation along this route precludes the description of a Queensland subspecies.

SPECIMENS EXAMINED

Varanus prasinus bogerti: AMNH 41693, Fergusson Island, d'Entrecasteax Archipelago.

Varanus prasinus prasinus: New Guinea — QM J2218, St. Joseph's River; AM R1205, no data; R6234, 'New Guinea'; R11492, R12533, Bulolo Valley; R16760, mouth of Oriomo River near Daru; R17963, 'Papua'; R24343, Fly River; R64790, Bristow Island near Daru; R65300, Daru Island, Western Province. Cape York — QM J31566, Buthen Buthen, Nesbit River; J35450, Leo Creek Road, 17 km NE. Mt Croll; J35451, Lankelly Creek, 10 km NE. Coen.

Varanus prasinus (subsp.?): QM J1190, Rossel or Russell Island New Guinea.

ACKNOWLEDGMENTS

Two of the specimens on which this work is based were collected by Mr R. Atherton and Mr K. McDonald of the National Parks and Wildlife Service while they were conducting fauna surveys

sponsored by the Australian National Parks and Wildlife Service and the Department of Environment, Housing and Community Development. Dr J. Winter co-ordinator of the surveys donated these two specimens to the Queensland Museum for Study.

Dr R. Zweifel (American Museum of Natural History) and Dr A. Greer (Australian Museum) made specimens in their care available for this work.

Assistance in translating Mertens' work has been received from Ms S. Maywald, Mr B. Hoffer, and Mr P. Davie.

Helpful suggestions in preparing the manuscript were made by Mr B. Campbell and Ms J. Covacevich (Queensland Museum), Dr A. Greer (Australian Museum), Mr G. Ingram (Queensland Museum), Dr G. Storr (Western Australian Museum), and Dr J. Winter (National Parks and Wildlife Service). I wish to thank Ms D. Fitton for typing the manuscript.

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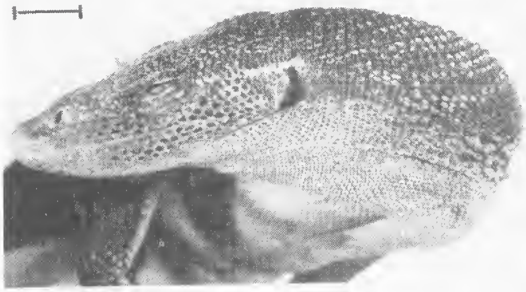
PLATE 1

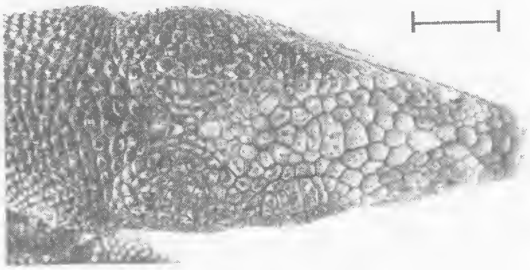
Varanus prasinus (QM J31566) Buthen Buthen, Nesbit River, Cape York Peninsula (scales in centimetres).

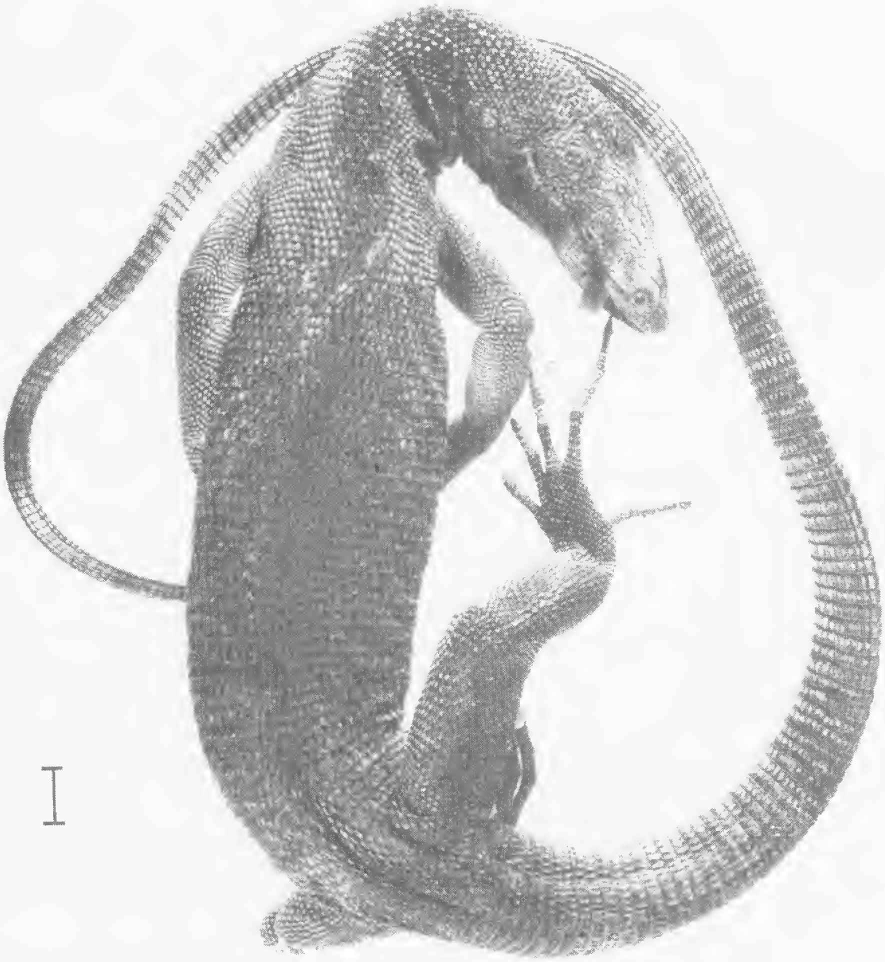
Top left: Lateral aspect of head.

Top right: Dorsal aspect of head.

Bottom: Dorsal view of body.







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A NEW FROG OF THE GENUS *TAUDACTYLUS* (*MYOBATRACHIDAE*) FROM MID-EASTERN QUEENSLAND WITH NOTES ON THE OTHER SPECIES OF THE GENUS

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ABSTRACT

Taudactylus liemi sp. nov. is described from montane rainforest mid-eastern Queensland. New data on the distribution and natural history of the other species of the genus (*T. acutirostris, T. diurnis, T. eungellensis* and *T. rheophilus*) are presented. A phylogeny has been devised for *Taudactylus* and aspects of the biogeography of the genus are discussed.

In 1975, the Australian Biological Resources Survey provided funds to enable the Australian and Queensland Museums to survey frogs and reptiles in rainforest sites of mid-eastern Queensland, as part of an overall survey of the rainforests of Queensland. The preliminary results of these surveys have been presented in Broadbent and Clark (1976), Queensland Museum (1976) and Covacevich (1977).

A large series of specimens of a new species was collected from two sites (Mt William and Crediton). These frogs were clearly referable to the genus *Taudactylus* because of the presence of T-shaped terminal phalanges (Fig. 1D), but were distinctly different from *T. eungellensis* described from the same area by Liem and Hosmer (1973). The new species is here described as *T. liemi*, in recognition of the contribution to herpetology made by Dr David Liem.

Measurements are in millimetres and ratios are expressed as percentages. Specimens are housed in the Queensland Museum (QM), and the Australian Museum (AM). Abbreviations follow Liem and Ingram (1977).

Taudactylus liemi sp. nov.
(Figs 1, Plate 1B)

MATERIAL EXAMINED

HOLOTYPE. Adult female, QM J32625, Crediton, ME.Q. (21° 12'S, 148° 33'E), 15–22 April 1975, collected by J. Covacevich, P. Filewood and R. Monroe.

PARATYPES. AM R47499–505, Mt William, 21–26 April, 1975, P. Webber; AM R47831, Eungella, 1975, P. Webber; QM J34420 18 km N. of Dalrymple Heights, December 1978, G.J. Ingram; QM J31515–8, Dalrymple Heights, 3 July, 1974, G. Czechura; QM J32618–24 (J32618 cleared specimen), J32626–33, J32660–8, J32694, same data as holotype.

DIAGNOSIS: Differs from *T. diurnis* and *T. eungellensis* by very small discs on fingers and toes; from *T. acutirostris* by the lack of dorsolateral skinfolds and in snout shape (in profile, rounded *vs* wedge shaped and curved upwards); and from *T. rheophilus* by the lack of extensive brown mottling ventrally, and by dorsal markings (presence of a dark triangle between the eyes and a dark lyre on the back). *T. rheophilus* is also more robust and has a larger HW/SWL. Liem and Hosmer (1973) give 37–42 for the latter whereas the range for *T. liemi* is 26–36.

DESCRIPTION OF HOLOTYPE: SVL 28·1, TL 11·7, TL/SVL 42, HW 8·4, HW/SVL 30, ED 3·1, ED/HW 37, EN 2·5, IN 3·4, EN/IN 74. Dorsal aspect of snout blunt, acuminate, rounded in profile. Loreal region sloping. Canthus rostralis distinct, curving in from eye and then out to nose, then converging anteriorly to form an acuminate snout. Pupil horizontal and oval shaped. Tympanum concealed. Tongue hinged in front, widest posteriorly where it is rounded; narrow and stright anteriorly. Vomerine teeth absent. Fingers unwebbed, slightly expanded distally. Length of

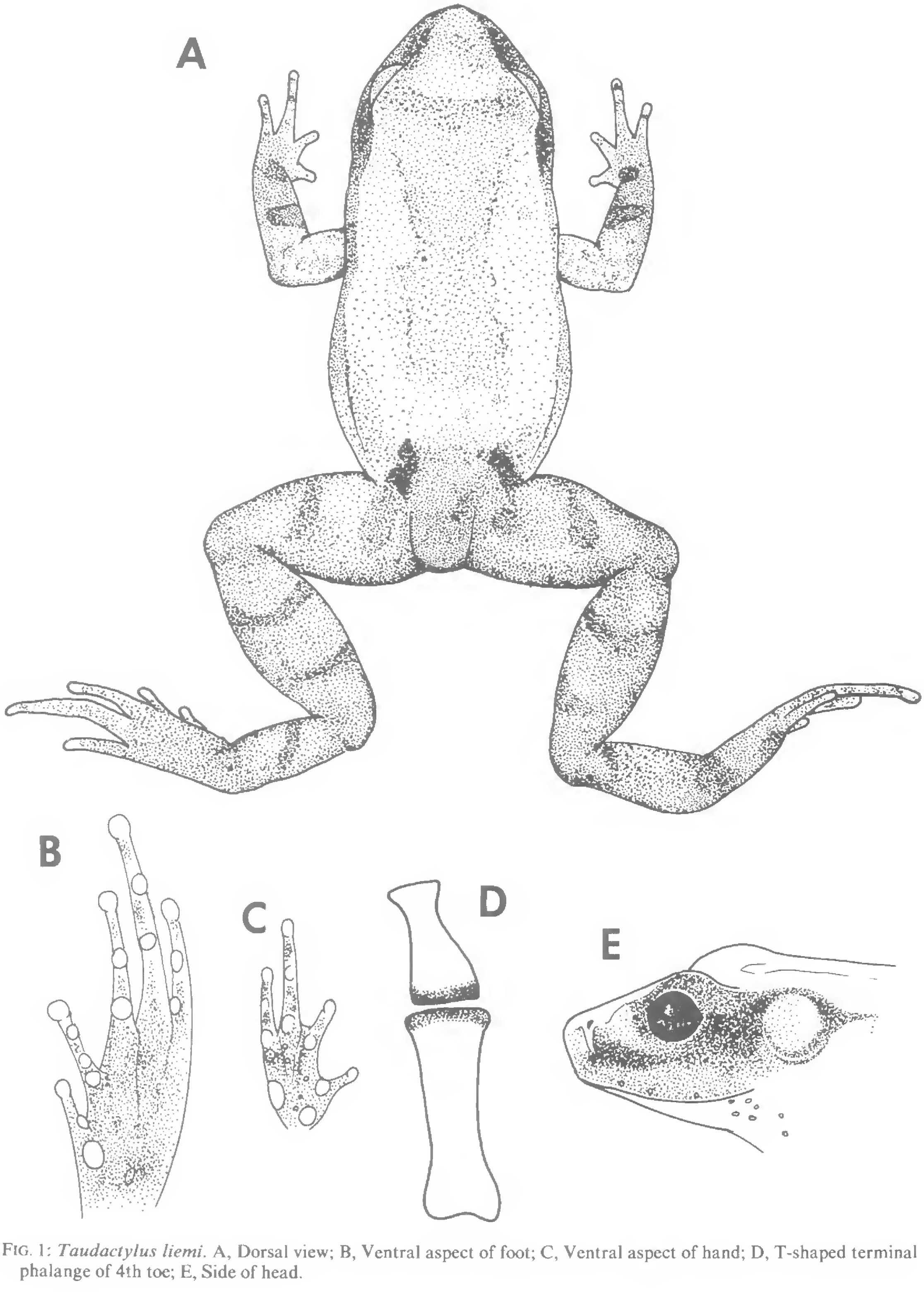

FIG. 1: *Taudactylus liemi*. A, Dorsal view; B, Ventral aspect of foot; C, Ventral aspect of hand; D, T-shaped terminal phalange of 4th toe; E, Side of head.

fingers shortest to longest 1–2–4–3. Large rounded tubercles at base of fingers; rounded outer palmer tubercle twice the size of oval inner tubercle. Toes not webbed but with distinct toe fringes, slightly expanded distally. Length of toes from shortest to longest 1–2–5–3–4. Low rounded tubercles at base of toes with smaller tubercles on joint above on 3rd, 4th and 5th toe; a small oval inner metatarsal tubercle. Skin smooth. Cloacal opening directed posteriorly at mid-level of thighs. Dorsal ground colour grey-brown; a black triangle between eyes, with the hypotenuse stretching from eye to eye and the apex directed backwards; a black lyre marking on neck and back; 'V' marking in front of hind legs with apex directed forwards; two cross bars on forearm, 8 on hind legs; fingers and toes barred. Laterally, ground colour grey-brown; a dark line from snout through eye and curving down into loreal region; side of face dark brown, lips barred; an indistinct dark upper lateral mark from above forelegs and fading at midbody; a dark blotch at beginning of foreleg and on knees. Posterior surface of thighs brown finely speckled with dirty yellow; black markings on either side of cloaca; heels dark. Ventrally, cream with fine brown speckling on legs.

DESCRIPTION OF PARATYPES: SVL 20·9–29·3 (N = 36, mean 26·1). HW 7·2–9·5 (N = 36, mean 8·4). HW/SVL 26–36 (N = 36, mean 32·0). TL 9·6–12·5 (N = 36, mean 11·5). TL/SVL 36–48 (N = 36, mean 44·2). ED 2·2–3·5 (N = 36, mean 2·9). ED/HW 27–44 (N = 36, mean 35·1). EN 2·0–2·5 (N = 36, mean 2·2). IN 2·8–4·0 (N = 36, mean 3·4). EN/IN 55–77 (N = 36, mean 65·5). Vocal sacs present in males. Dorsal and lateral colouring varies from light brown to dark brown when ground colour very dark the markings can be difficult to discern, and when light, they can be faint. Lyre marking on back can extend forward joining up with the triangle between the eye and it can extend backwards breaking up into blotches in front of the 'V' marking in front of the cloaca. Apex of this 'V' is often missing. The hidden tympanum may be defined by a light patch. The upper lateral stripe in some specimens extends backwards and down to the inguinal region. Ventrally there may be more intense brown speckling. Nasal bones narrow, widely separated and not touching sphenethmoid or the maxillary; frontoparietal fontanelle moderately large; zygomatic rami of squamosal as long as otic rami; omosternum present; sternum rounded; terminal phalanges of fingers and toes T-shaped (Fig. 2B).

HABITAT: Rocky streams and their environs in montane rainforest.

DISTRIBUTION: Eungella area west of Mackay, ME.Q., from Mt. William in the north to Crediton in the south.

FIELD NOTES: *T. liemi* is a secretive frog. Males call on land under rocks along the side of rocky streams. In December 1978, they called all day but more commonly at night. G. Czechura (pers. comm.) noted in July 1974 that they were calling in large numbers. There appeared to be no difference between the numbers calling day or night. He found them mostly under rocks during the day and under roots and in the mouth of crayfish burrows during the night. Amplexus was noted as inguinal. In August 1976, he heard no vocalization. At Crediton, in April 1975, individuals were caught inside the rolled up ends of palm fronds (*Archontophoenix* sp.) in an area where no running streams were observed (J. Covacevich, pers. comm.). A number of these individuals were gravid females. The trunk ends of these palm fronds have moist micro-environments inside and are a catchment for water during rain. Gravid females carry 34–51 large eggs measuring 1·7–2·5 mm. Egg masses and tadpoles have not been identified.

Species synchronosympatric with *T. liemi* were *Adelotus brevis, Taudactylus eungellensis, Mixophyes fasciolatus, Litoria chloris* and *L. lesueurii*.

CALL: To the ear the call is a short series of 'tinks'. A sound spectograph of this call is given in Plate 1(B). This is based on a recording by Chris Corben at Dalrymple Heights, Eungella, ME.Q., in January 1976. The energy of the call is concentrated between 3000–4000 HZ, and has a duration of 411 milliseconds. It is composed of 4 pulses, with an individual duration of 81 milliseconds. The number of pulses however, may vary between 1 and 6 but 3 predominates. An individual calls on the average 27 times per minute. The call is easily distinguished from the multipulsed, sharper 'ting' call of *T. rheophilus*, the long multipulsed 'eek, eek, eek . . .' call of *T. acutirostris*, and the soft, short 'eek eek eek' call of *T. diurnis*.

NOTES ON THE OTHER SPECIES OF *TAUDACTYLUS*

Frogs of the genus *Taudactylus*, Straughan and Lee (1966), occur only in isolated montane

rainforest of eastern Queensland, south of Mt Hartley, some 20 km south of Cooktown. They are a conspicuous element of the rainforest fauna where ever they occur, and are almost invariably associated with cool, clear, fast-flowing rocky mountain streams. Three species are sun-loving and diurnal, an unusual habit amongst frogs. Two species have high pitched, very distinct, bell-like calls.

The most recent work on this genus was undertaken by Liem and Hosmer (1973). Since that study, new data on the natural history and distribution of the four previously known species have been compiled. These are summarized below.

T. acutirostris (Andersson 1916)

DISTRIBUTION: Great Dividing Range, north-eastern Queensland from Mt Hartley, Bloomfield area in the north, to Tully Falls in the south.

CALL: To the ear, the call is a series of 'eek-eek-eek . . .' sometimes ending or beginning with sharp metallic notes. Plate 1(c) is a sound spectograph of part of a call based on a recording by the author at Mt Lewis on 7 Nov., 1975. The call has a dominant frequency of 3000 HZ and the pulses have an individual duration 63 milliseconds. The call is usually from 4–6 seconds long with 17–25 pulses per call. An individual calls on the average 7 times per minute. Males form a chorus.

FIELD NOTES: *T. acutirostris* is mainly active during the day especially on sunny days when they will often 'bask' in the sun. Males call exposed on rocks and will interrupt calling when clouds move in front of the sun. Typically, after a period of exposure on a rock in the sun, individuals move off to forage along the sides of creeks and on the rainforest floor nearby. When distrubed they show no hesitation in jumping into water, be it a still pool or a waterfall. In still pools they lie exposed on the bottom amongst the leaf litter or rocks for several minutes before resurfacing.

COMMENTS: There is much confusion in the literature regarding the call of this species. Clyne (1969) calls it the Tinker Frog and gives the call as a series of metallic 'tinks'. Liem and Hosmer (1973) describe the call as a series of sharp tapping sounds repeated 3–4 times in quick succession. Neither have been verified by further field observations. Males typically call in a chorus sometimes giving sharp metallic notes at the beginning and end of calls but especially during male-male aggression. The typical call of *T. acutirostris* has been recorded at the upper reaches of Mulgrave River and Charmillan Creek, Ravenshoe (G. Czechura pers. comm.).

T. eungellensis Liem and Hosmer, 1973

DISTRIBUTION: In the ranges west of Mackay, ME.Q., from Clark Range in the north (A. Greer pers. comm.) to Finch Hatton Gorge and Credition in the south.

CALL: Liem and Hosmer (1973) record the call of this species as a high pitched metallic tinkering noise, like a little hammer tapping on metal repeated 4–5 times in quick succession. This has not been verified either by my own field observations or by C. Corben and G. Czechura (pers. comms.). Indeed we have failed so far to discover if it calls at all. *T. liemi* is synchronosympatric with *T. eungellensis* and was at that time undiscovered. It appears Liem and Hosmer have confused the two, and their description may apply to the *T. liemi* call. It would be surprising if a frog without vocal sacs could produce a high pitched, sharp tinkering call.

FIELD NOTES: *T. eungellensis* is similar in behaviour to *T. acutirostris* except in the case of calling males.

T. rheophilus Liem and Hosmer, 1973

DISTRIBUTION: Great Dividing Range, NE. Q., from Thornton Peak, Daintree area, in the north to Mt Lewis in the south.

CALL: To the ear, the call is a series of sharp metallic 'tink-tink-tink . . . . . Plate 1(A) is a sound spectograph of the call based on a recording by the author at Mt Lewis on 6 December, 1975. It shows a dominant frequency of 5500 HZ and a lower harmonic containing nearly as much energy around 2750 HZ. The pulses have an individual duration of 31 milliseconds. The call is usually between 4–5 seconds long with 11–15 pulses per call. On the average an individual will call 5 times per minute.

FIELD NOTES: This species is a very secretive frog. It calls day and night but mainly during the day. Male calling sites are usually under rocks or roots and individuals may be partly in water. Calls form a chorus.

T. diurnis Straughan and Lee, 1966

DISTRIBUTION: Conondale Ranges (Czechura 1975) and Blackall Ranges in the north to Mt Nebo, D'Aguilar Range in the south.

CALL: As Liem and Hosmer (1973) have noted, males do not have vocal sacs but can vocalize. This is especially evident in captivity. To the ear, the call is soft 'eek-eek' sometimes with sharper notes, and is reminiscent of *T. acutirostris*. In the field, the call is heard especially during male-male aggressive encounters. No breeding choruses have been noted.

FIELD NOTES: *T. diurnis* and *T. eungellensis* are very similar in behaviour. Individuals forage into late evening.

PHYLOGENY

The following characters were used in the preparation of Table 1, and the construction of the cladogram (Fig. 2). These show the relationships between the five species of *Taudactylus*. The data for species other than *T. liemi* are taken from Liem and Hosmer (1973). (1) represents the apomorphic character-state and (0) the plesiomorphic character-state.

TABLE 1: CHARACTER-STATES OF THE SPECIES OF *TAUDACTYLUS*.

Species	Characters 1	2	3	4	5	6	7
T. diurnis	0	0	1	1	1	1	1
T. eungellensis	0	0	1	1	1	1	1
T. acutirostris	1	1	0	0	0	0	1
T. rheophilus	1	1	0	0	0	0	1
T. liemi	1	1	0	0	0	0	1

0 = plesiomorphic, 1 = apomorphic.

1. EXPOSURE OF FRONTOPARIETAL FONTANELLE: Following the reasoning of Lynch (1978), the lack of an exposed fontanelle, or the presence of a very small fontanelle (1), is considered to be apomorphic and an extensive fontanelle (0), plesiomorphic.

2. NASALS CONTACTING THE MAXILLARY: Large nasals contacting the maxillary (0) are considered to be plesiomorphic, and small nasals not contacting (1), apomorphic.

3. OMOSTERNUM: Liem and Hosmer (1973) are followed in considering the lack of an omosternum (1) apomorphic, and presence (0), plesiomorphic.

4. VOCAL SACS: Because most male frogs possess vocal sacs, the absence of sacs (1) is considered apomorphic, and presence (0), plesiomorphic.

5. DIGITAL DISCS: Liem and Hosmer (1973) are followed in considering broad digital discs (1) as apomorphic, and narrow discs (0) as plesiomorphic.

6. SUBARTICULAR TUBERCLES OF FINGERS: Liem and Hosmer (1973) regarded absence of these tubercles (1) as apomorphic, and their presence (0) as plesiomorphic.

7. T-SHAPED TERMINAL PHALANGES: The T-shaped terminal phalanges is unique to *Taudactylus* and is thereby considered autoapomorphic (1) for the genus.

From the cladogram in Figure 2, it can be seen that there are two sister groups in *Taudactylus* — the *T. diurnis* complex *(T. diurnis* and *T. eungellensis)* and the *T. acutirostris* complex *(T. acutirostris, T. rheophilus,* and *T. liemi)*. The latter group is presented as a trichotomy. Dichotomies are to be preferred; however, unless they are supported by characters, they are invalid (Platnick and Shadab 1978).

The *T. diurnis* complex is regarded as apomorphic because it contains more apomorphies than its plesiomorphic sister group, the *T. acutirostris* complex (Table 1).

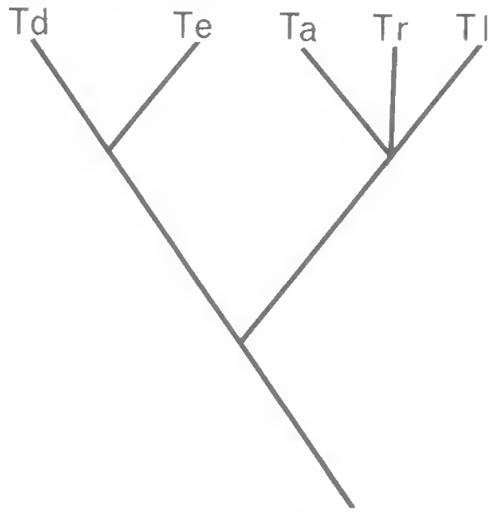

FIG. 2: Cladogram of the species of *Taudactylus*. Td = *T. diurnis*, Te = *T. eungellensis*, Ta = *T. acutirostris*, Tr = *T. rheophilus*, Tl = *T. liemi*.

BIOGEOGRAPHY

Hennig (1966) has stated that sister groups should be allopatric and that the most primitive sister groups remain near the centre of origin of the overall group. The *T. acutirostris* complex is the pleisiomorphic sister group, and is centred in northeast Queensland. Thus, it would seem reasonable to assume that this area was the centre of origin of the genus *Taudactylus*. Probably, the *T. diurnis* complex evolved from a *T. acutirostris* complex-like ancestor that invaded the rainforests of southern Queensland and became isolated there during rainforest contractions. Later, as the rainforest once again extended, the *T. diurnis-eungellensis* ancestral group may have reinvaded northern Queensland, and again become isolated by subsequent contractions, such that a northern group *(T. eungellensis),* and a southern group *(T. diurnis)* were formed. The ancestor of *T. liemi* may have been similarly isolated by rainforest contractions in mid-east Queensland.

It is difficult to reconstruct the evolution *T. acutirostris* and *T. rheophilus* with an allopatric model. The latter is synchronosympatric with the former, although *T. acutirostris* is distributed a little further north and south, and occurs at lower altitudes.

T. rheophilus and *T. liemi* are restricted to areas that acted as rainforest refugia (Mt Lewis, Thornton Peak, Eungella — Webb and Tracey, in press) during dry periods of the Pleistocene. The other species, although having important refugia within their range, have colonized rainforest areas nearby.

No species of *Taudactylus* occur in New Guinea or in rainforests north of the Daintree River 'block'. This is not surprising as it is unlikely that the high altitude, clear cool, fast-flowing rainforest streams necessary for *Taudactylus* existed during the dry Pleistocene periods when land connections were extant (Kikkawa, Monteith, and Ingram, in press; Covacevich and Ingram, in press).

ACKNOWLEDGMENTS

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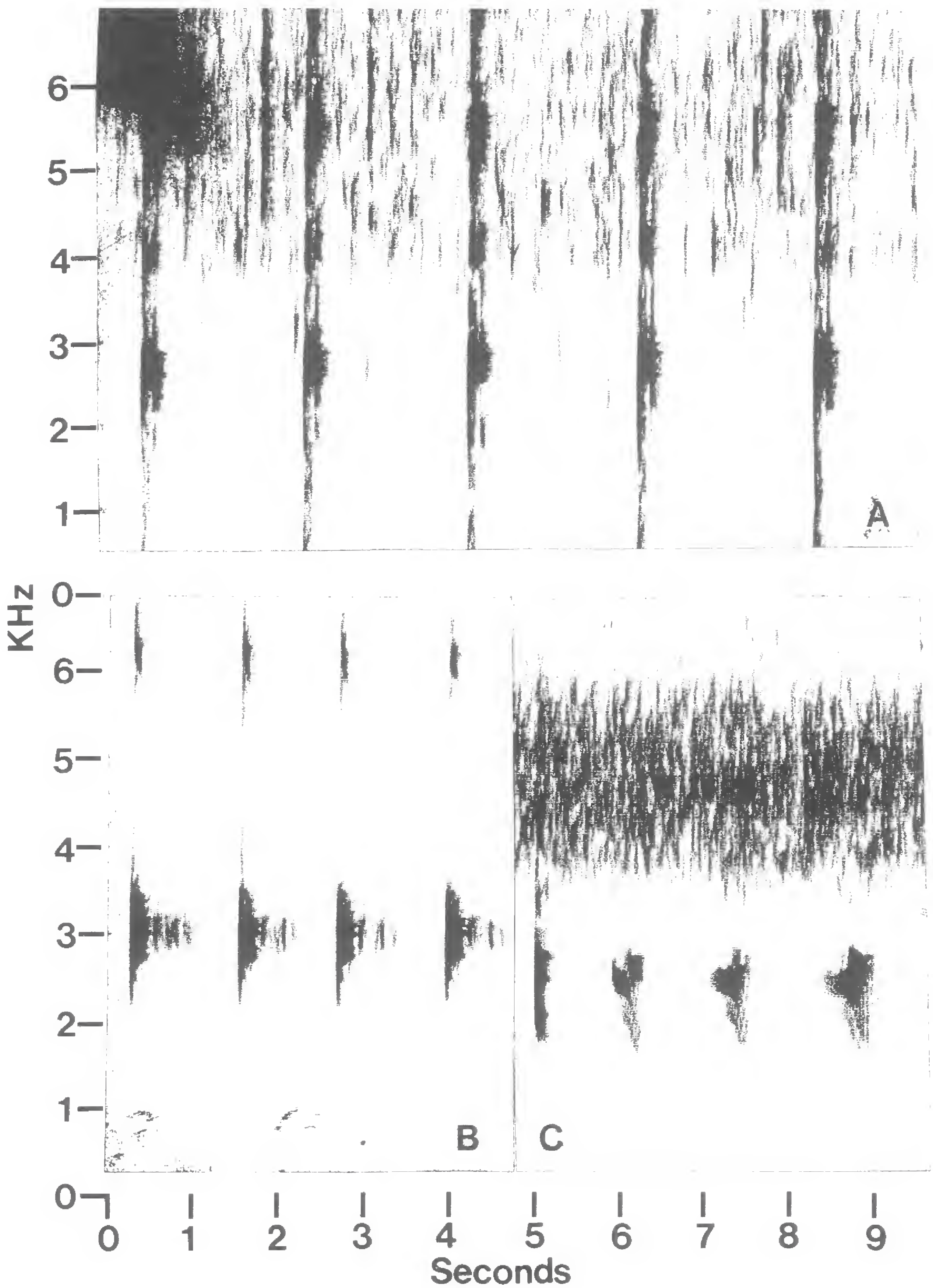
PLATE I

Sonographs of the calls of *Taudactylus*.
A: *T. rheophilus*
B: *T. liemi*
C: *T. acutirostris*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RADIOGRAPHIC PATHOLOGY IN MANDIBLES OF *ANTECHINOMYS LANIGER* FROM HORSESHOE CAVE, WESTERN AUSTRALIA

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ABSTRACT

Jaw fragments of *Antechinomys laniger* (Gould) were radiographed. It was found that the cave population contained mature animals and a number of older individuals with dentitions at the end of their functional period due to excessive wear.

A number of mandibles of *Antechinomys laniger* (see Archer 1977 for revision of the genus) collected by Dr M. Archer from Horseshoe Cave (N59), on the Western Australian Nullarbor, in February 1970, have been radiographed. One is Queensland Museum number J23103; the others have no acession numbers. Jaw fragments were radiographed from both sides using fine grain photographic film and a modified dental radiographic apparatus with the aluminium filter removed (Miller and Radnor 1970).

RESULTS

Judging by the presence or absence of teeth, and the wear on the occlusal surface, individuals were either mature adults or old adults.

MATURE ANIMALS: The jaw fragments mostly contained the post-canine dentition: P_{1-3} and M_{1-4} were present. When viewed bucco-lingually all teeth appeared to be two rooted: the premolars slightly shorter than the molars. The premolar cusp pattern was also simpler.

With increasing occlusal tooth wear, presumably associated with increase in age, it may be observed (Plate 1) that the cheek teeth have migrated occlusally so that the distance between root-apex and lower border of mandible has increased. There is also an increase in the distance between the bifurcation of the root and the tip of the alveolar crest in some teeth. The roots, however, appear to be otherwise correctly seated in their bony sockets so that one may assume this to be biological rather than artefactual, but probably pathological. The most likely cause is that it is due to the loss of bone, associated with periodontal inflammation, during life.

The horizontal distance between the distal surface of M_4 and the ascending ramus of the mandible was larger in animals with the most wear. This implies that some type of physiological mesial drift has taken place with age. This is a process which is more marked in macropodids, namely molar migration.

OLD ADULT ANIMALS: Partially edentulous jaws were of two kinds. One type had lost teeth almost certainly *post mortem*. The sockets were clearly visible on the radiographs. The remaining teeth were incompletely embedded in bone, and this would facilitate *post mortem* loss of teeth. The sockets of all teeth were at a comparable level however, implying similarities in the teeth and their supporting structures *ante mortem*.

One jaw (J23103) had considerable *ante mortem* tooth loss (Plate 1A). It so happened that C_1 and a fragment of I_3 were also present. Only three molars were still in the jaw. M_4 was severely worn and extruded to a certain degree. Bone loss around the distal root and bifurcation was considerable, with cratering behind the tooth and an inflammatory sclerosis in the bone behind M_4 as indicated by increased radiodensity. M_3 and M_2 were severely worn but their bony support within normal limits. M_1 was lost but its socket was still visible although abnormal in outline. The mesial part was much wider than normal and rounded in outline and the distal slightly so. A dark oval area can be seen on the radiograph related to the mesial root which on the bone was an open buccal sinus

about 2 mm in diameter. This should be termed a sinus and not a cloaca, the latter term is usually associated with the much more severe inflammatory changes and bone necrosis of osteomyelitis when the marrow cavity is also severely effected by the inflammatory process and the periosteum has been stripped from the bone, due to the presence of migrating pus, to subsequently give rise to a new bone known as an involucrum. The remaining cheek teeth P_{1-3} were missing but odd irregularities in bone density indicate that they had been present but were lost sometime *ante mortem*.

The most distal missing tooth is identified as M_1 because no space is found behind the terminal molars to accommodate another tooth, and the socket depth indicates a root length similar to the other molar teeth. When the tooth row is complete (P_1–M_4), the premolar root length is distinctly shorter than that of the molars. This may be observed on other specimens on the radiograph.

Discussion

Although inflammatory jaw bone diseases are relatively common in animals in captivity they are rare in wild animals (Colyer 1936, Potkay 1977). Such is the importance of the dentition that a defect such as these usually results in the death of the animal.

This cave population (Horseshoe Cave N59) contained a number of older individuals with dentitions at the end of their functional period due to excessive wear and one with considerable tooth loss, one quadrant being almost nonfunctional. It is most unusual to find populations with this degree of nonfunction. One might ask whether these were the remains of old individuals killed by some predator and subsequently dumped or maybe stored in the cave. Associated with this it is likely that the oldest specimens were the longer lived females at the end of the breeding season. From their dentitions alone they would be incapable of much extension of their life span. This is relatively recent material (pers. comm. M. Archer) so one might expect the post cranial skeleton to be present if natural death had occurred. The finding of mostly dentary fragments also argues for the effects of a predator on exhausted animals at the end of the short life span.

ACKNOWLEDGMENTS

I must thank Dr M. Archer for making this material available for study. Travel support in part by a Grant in Aid from Melbourne University and Departmental funds, Dental Surgery and Medicine, School of Dental Science, University of Melbourne where the author was on sabbatical leave.

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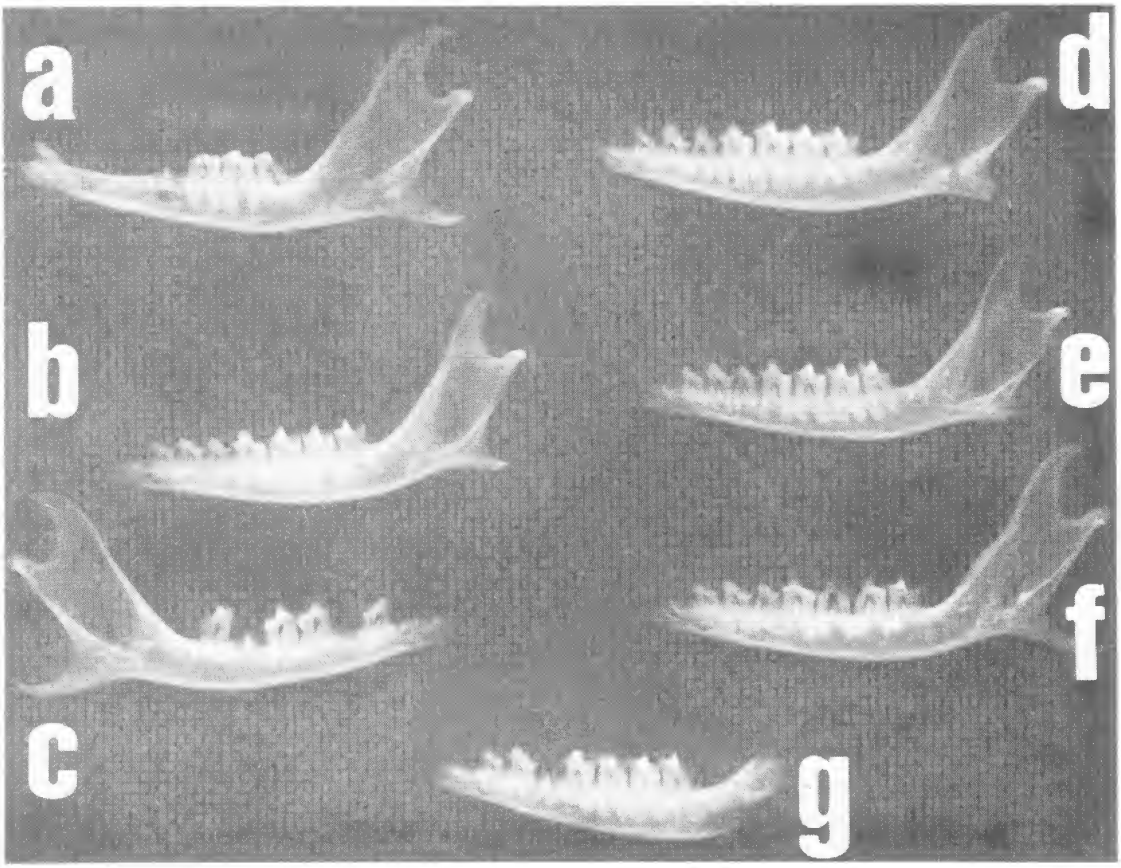

PLATE 1

Radiographs of seven dentaries of *Antechinomys laniger* collected by Dr M. Archer at Horseshoe Cave. All of right side except C. Compare D with F to appreciate movement of teeth away from lower border of the bone with increased wear on the cheek teeth. Shorter tooth roots of premolar teeth are evident. A is J23103.

Mem. Qd Mus. **20**(1): 125–33, pl. 1 [1980].

TWO LARGE AUSTRALIAN ORB-WEAVING SPIDERS, *ERIOPHORA TRANSMARINA* (KEYSERLING 1865) AND *ERIOPHORA BIAPICATA* (L. KOCH 1871)

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Queensland Museum

ABSTRACT

Eriophora transmarina and *E. biapicata* have been re-described. A neotype has been established for *E. biapicata*. *E. transmarina* is found along the eastern coast of Australia from New South Wales to New Guinea. *E. biapicata* occurs in the western areas of the eastern states, in Central, South and Western Australia.

There has been continual confusion about the identity of the large orb-weaving spiders in Australia. The controversy has mainly centred on *Eperia transmarina* Keyserling 1865 and *Epeira producta* Koch 1867. Koch (1871) redescribed and figured ♂ and ♀ *E. producta* from Brisbane as well as ♀ *E. transmarina* from localities in Queensland and New South Wales. Keyserling (1886) believed *E. producta* to be a synonym of *E. transmarina.* He redescribed and figured ♂*E. transmarina* and believed *E. transmarina (sensu* Koch) to be a new species, *E. annulata;* this spider has a short epigyne and may be penultimate. It was synonymised with *Araneus heroine* by Dondale (1966). The *Epeira* spp. were transferred to *Araneus* by Simon (1895, p. 800). Hogg (1900) and Rainbow (1909, 1911) recognised that there were at least two large *Araneus* spp. Chrysanthus (1960) discussed the problem and the literature in detail and decided that the New Guinea species was *A. productus* and that *A. transmarinus* was probably a separate species. Dondale (1966) examined the type specimens from Hamburg and figured specimens from Canberra. He concluded that *A. productus* was a synonym of *A. transmarinus.* Chrysanthus (1970) agreed with Dondale's findings. Since then the view that there was only one very large orb-weaving spider, *Araneus transmarinus* that was found over the whole of Australia has been current (Main 1976). However large male spiders which differed from *A. transmarinus* by the possession of spurs on both coxae I and II had been collected from the western areas of Queensland. An examination of Dondale's description of ♂ *A. transmarinus* from Canberra reveals that it also bears a spur ventrally on coxae II (in all other descriptions of *A. transmarinus* there is a spur on coxa I only.)

To clear up this problem specimens of these large *Araneus* held in overseas collections were examined as well as specimens from museums in Australia and New Zealand. Archer (1951) assigned both species to *Eriophora* and Levi (1970) mentions the presence of this genus in Australia and New Zealand. Much earlier Musgrave (1933) had published a leaflet describing the garden orb-weaving spider of Sydney as *Eriophora transmarina.*

Material from the following museums has been examined: Zoologisches Staatinstitut und Zoologisches Museum, Hamburg (ZMH); British Museum Natural History (BM); Forschungsinstitut Senckenberg, Frankfurt (SMF); Zoologisches Museum Humboldt Universitat, Berlin (ZMHU); Canadian National Collection of Insects, Ottawa (CNC); Otago Museum, Dunedin (OM); National Museum, Melbourne (NM); Australian Museum, Sydney (AM); South Australian Museum, Adelaide (SAM); West Australian Museum, Perth (WAM); Australian National Insect Collection, Canberra (ANIC).

Eriophora Simon 1864

The posterior part of the abdomen is generally high above the spinnerets. There are often

posterior and dorsal tubercles on the abdomen. The lateral eyes of the males are on a dorsal stalk, the medians on a projection. The chelicerae are concave anteriorly, providing space for the large palpal organs. The patellae of the ♂ palps have 1 apical spine, 1 spine and a companion hair, or rarely 2 spines as in *Araneus* (Archer 1951). Coxae I have a hook on the distal margin; tibiae II are modified. In the ♂ palp the median apophysis is transverse and elongate with acute or sub-actue spurs, blades or lobes. The radix, embolus and conductor are elongate. A paramedian apophysis is present by which it may be distinguished from *Araneus* (Levi 1970). The cymbium is narrow and canoe-shaped. The epigynum usually has a long scape which is attached to the anterior of the base and bends backwards; the openings are ventral under the scape.

Eriophora spp. from Australia are large and hairy; there are 2 dorsal longitudinal bald lines on the tibiae. The spiders construct large orb-webs which have widely spaced spirals and open hubs.

Eriophora transmarina (Keyserling 1865)

Epeira transmarina Keyserling, 1865, p. 814; 1886, p. 139.
Epeira producta Koch, 1867, p. 178; 1871, p. 55. Thorell, 1881, p. 90.
Araneus productus: Simon, 1895, p. 800. Rainbow, 1909, p. 222; 1911, p. 190. Roewer, 1942, p. 831. Chrysanthus, 1960, p. 30; 1970, p. 33.
Araneus transmarinus: Rainbow, 1911, p. 195. Roewer, 1942, p. 834. Bonnet, 1955, p. 613.
Eriophora transmarina: Musgrave, 1933, p. 1. Archer, 1951, p. 21.
Eriophora producta: Archer, 1951, p. 21.

MATERIAL EXAMINED

2 ♂ (paratypes) *Epeira transmarina* Rockhampton (ZMH); ♀ ♂ *Epeira producta* Sydney (BM); 2 ♂ ♀ *Eriophora transmarina* Mt Greville, SEQ, G. May 24.iii.1974 QM S356, S357, S358 (figured); ♂ *E. transmarina* Brisbane, SEQ, V.E. Davies 11.ii.1979 QM S360 (SEM); ♀ *E. transmarina* Bald Hills, SEQ, A. Carseldine 5.ii.1979 QM S359 (figured).

As well as these 29 ♂♂ and over 100 ♀♀ of these common large spiders from the AM and QM collections were examined.

DESCRIPTION

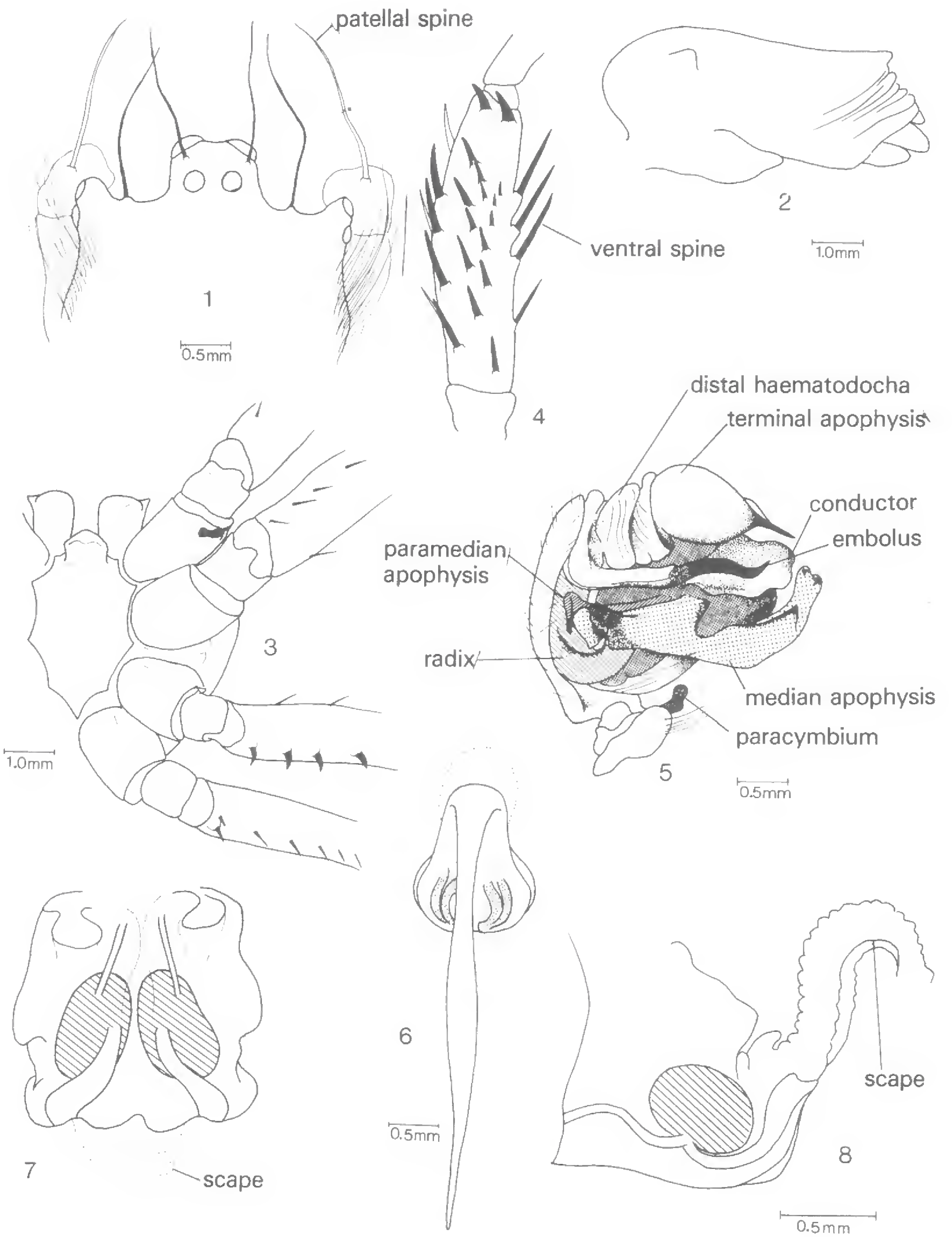
MALE: Length 13–17 mm. Two long setae on the anterior edge of the cephalothorax between the median and the lateral eyes; 2 long setae between median eyes. The posterior median eyes are smaller than the anterior median eyes, (Fig. 1) and an equal distance apart. There are 2 latero-dorsal tubercles and a posterior tubercle on the abdomen. Under this there may be folds around the hind end of the body but no distinct tubercle (Fig. 2). There is a hook on the distal margin of coxa I but none on coxa II (Fig. 3). All males examined have 4 ventral thorn-like spines on femur III and 7–9 retroventral spines on femur IV. Tibia II is swollen prolaterally. It has 3 spines dorsally, 3 large spines and 1 or 2 small spines ventrally and 16–19 prolateral spines, 2 of which are apical and 4 of which may be regarded as upper prolaterals; the lower prolaterals vary in number between 10 and 13 (Fig. 4). ♂ palp (Fig. 5, Plate 1B); see also Chrysanthus (1960, Fig. 47). The paramedian apophysis arises as a proximal extension of the conductor.

FEMALE: Length 18–26 mm. The pattern is extremely variable as noted by all previous authors. The cephalothorax is covered with long hairs (Plate 1A). The lateral eyes are not on a stalk and there are no long setae on the anterior edge of the cephalothorax. The posterior median eyes are smaller and closer together than the anterior median eyes. The clypeus is about 1·5x the diameter of an anterior median eye. The length of the scape is 3·5–4·9 mm (average 4·3). There are 4–6 (rarely 3 or 7) proventral spines on femur II. Epigynum (Fig. 6, 7, 8) see also Chrysanthus (1960, Figs. 64, 71).

DISTRIBUTION: *E. transmarina* is found along the eastern coast of Australia from New South Wales to Cape York Peninsula (Fig. 16) and in eastern New Guinea.

BIOLOGY: The spiders construct large vertical or near vertical orb-webs which have widely spaced spirals and open hubs. The webs are 70–120 cm in diameter measured across the outermost spiral and are usually elliptical with the longest axis vertically. The open hub varies between 2 and 5 cm and may be circular or elliptical; it is in the upper half of the web. The number of spirals is variable; the space between spiral threads is 6–18 mm. The number of radials appears to be fairly constant at 17–20. Though the web is usually left up during the day no kleptoparasites have been seen. The spider rests under leaves to the side or above the web. The egg coccoon which is covered in woolly green-brown silk is placed in a few loosely bound leaves.

Males and females are most plentiful in summer especially in January and February but stray adults have been collected throughout the year. From about March the eggs hatch and the spiders overwinter as juveniles to mature the following summer.



FIGS. 1–5: ♂ *Eriophora transmarina* (QM S356, S357). 1, anterior cephalothorax, dorsal; 2, abdomen, lateral; 3, cephalothorax, ventral; 4, l. tibia II, prolateroventral; 5, l. palp, mesal.
FIGS. 6–8: ♀ *Eriophora transmarina* (QM S358, S359). 6, epigyne, ventral; 7, epigyne, posterior; 8, epigyne, lateral.

Eriophora biapicata (L. Koch 1871)

Epeira biapicata Koch, 1871, p. 54.
Araneus biapicatus: Rainbow, 1911, p. 182. Bonnet, 1955, p. 422.
Aranea producta: Strand, 1913, p. 608 [not *Epeira producta* Koch, 1867, p. 178].
Aranea biapicata: Roewer, 1942, p. 825.
Araneus transmarinus: Dondale, 1966, p. 1164 [not *Epeira transmarina* Keyserling, 1865, p. 814].

TYPE MATERIAL

It has been confirmed by the Naturhistorisches Museum, Stuttgart that the ♀ holotype of *Epeira biapicata* Koch 1871 was destroyed during World War II bombing raids. As the immature specimens from Fiji were doubtfully associated with the nominal species (Koch, 1871, p. 55) they can not be considered part of the type series (ICZN, Article 72b). A male has been chosen as the neotype as the female lacks good diagnostic characters (ICZN, Article 75c, 4). Koch separated the large *Epeira* spp. into those with and those without longitudinal grooves or bald lines on the tibiae. *E. biapicata* fell into the former group which was further divided on the presence or not of a tubercle below the hind point of the abdomen. *E. biapicata* and *E. thryidota* have this tubercle. The types of the latter have not been located.

MATERIAL EXAMINED

NEOTYPE ♂, *Eriophora biapicata,* mulga scrub, 64 km west Westmar, SCQ, R. Raven, V. Davies, 9.i.1979, QM S361; ♂♀♀ *Aranea producta,* Central Australia, SMF; ♂ *Araneus transmarinus* det Dondale, Canberra, A.C.T., C.R. MacLennan, 13.ii.1963, CNC; ♀ *A. transmarinus,* Canberra, AM; juvs *A. transmarinus,* Canberra, 5.ii.-15.v.1963, ANIC: 7 ♂, Perth, W.A., WAM 77/489, 78/1, 78/5, 78/10, 78/11, 78/12, 78/14; ♂, Bunbury, W.A., WAM 78/6; ♀, Karrinyup, W.A., WAM 77/490; 2 ♂, Melbourne, Vic., NM; ♀, *A. transmarinus* det. Hogg, S. Brighton, Vic, NM; ♀, Caldwell, N.S.W., NM; 5 ♂, Adelaide, S.A., SAM 5327; ♀, ♂, Murray R. between Blanchtown and Swan Reach S.A., SAM 5327; ♂, Winton, WCQ, QM S362; ♂, 2 ♀, juv, 64 km west Westmar, SCQ, QM S363; ♀, 64 km west Westmar, SCQ, QM S364; ♂, Woodridge, Brisbane, SEQ, QM S365; 2 ♂, Mt. Pleasant, Dalby, SEQ, QM S366; ♂, Mt. Colliery, SEQ, QM S367; ♂, Goondiwindi, SEQ, QM S368; 2 ♀, juv., Kumbarilla, SEQ, QM S369; ♀, College View, via Gatton, SEQ, QM S370; ♀, Cunnamulla, SWQ, QM W1477; ♀, Longreach, CQ QM S371; 3 ♀, Canberra, A.C.T., QM S372; ♂, Eastwood, N.S.W., AM KS3144; ♀, Broken Hill, N.S.W., AM KS3145; ♀, Ardlethan, N.S.W., AM KS3146; ♀, Menindee, N.S.W., AM KS3147; ♀, Bingara, N.S.W., AM K61643; ♀, Strathfield, Sydney, N.S.W., AM K56167; ♀, Canterbury, Sydney, N.S.W., AM KS3148; ♀, Mandurama, N.S.W., AM KS3149, ♀, Earlwood, N.S.W., AM K66688; ♀, Woy Woy, N.S.W., AM KS3150; ♀, Campsie, Sydney, N.S.W., AM K61645; ♀, Katoomba, N.S.W., AM K56200; Putney, Sydney, N.S.W., AM K57451; ♀, Bexley, Sydney, N.S.W., AM K55478; ♀, Willoughby, Sydney, N.S.W., AM K57602; ♀, Lithgow, N.S.W., AM K53530; ♀, Wahroonga, Sydney, N.S.W., AM K61649; ♀, Dundas, N.S.W., AM KS3151; ♀, Naremburn, N.S.W., AM K61120; ♀, Mudgee, N.S.W., AM KS3152; ♀, Annangrove, N.S.W., AM KS3153; ♀, Northam, W.A., AM KS3154.

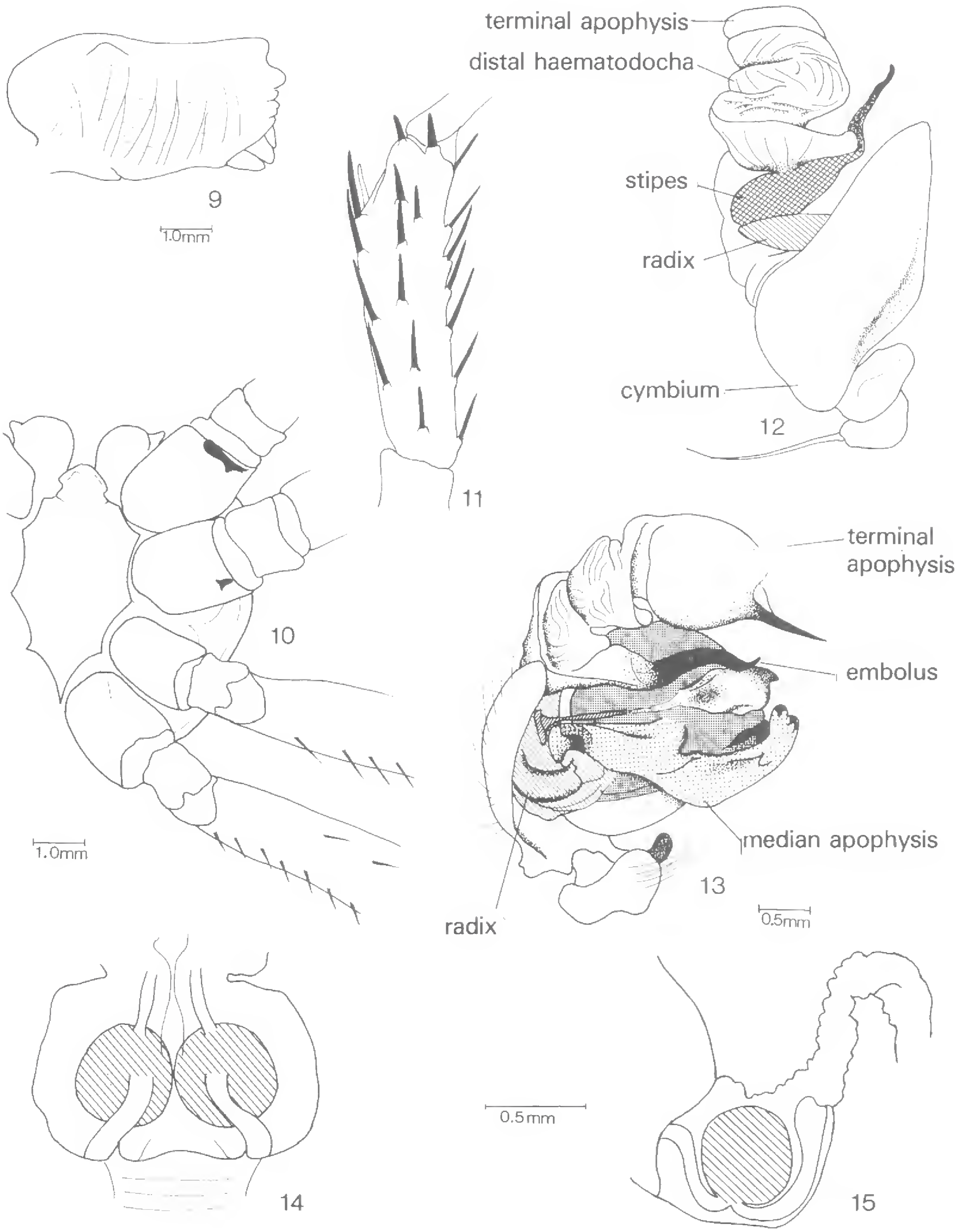
DESCRIPTION

MALE NEOTYPE: QM S361: Cephalothorax length 10·0 mm; abdomen length 12·8 mm; total length 19·0 mm. There are 2 long setae on the anterior margin of the cephalothorax between lateral eyes and median projection; 2 long setae between the anterior and posterior median eyes. The latter are smaller than the anterior eyes 5:6; the eyes are an equal distance apart. The abdomen has 2 latero-dorsal tubercles, a posterior one and another posterior tubercle below this (Fig. 9). There is a distal ventral hook on coxa I and a distal spur on coxa II (Fig. 10) as noted by Dondale (1966). There are 5 spines on femur III and 9 retro-ventral spines on femur IV. Tibia II is swollen prolaterally. It has 3 dorsal spines, 7 ventral spines and 12 prolateral spines — 2 apical, 4 upper and 6 lower prolaterals (Fig. 11). ♂ palp (Figs. 12, 13); see also Dondale (1966, fig. 2G). This is very similar to *E. transmarina* however the terminal apophysis is relatively larger.

VARIATION: Males examined varied in length from 11 to 19 mm. The abdomen is either uniform in colour or has a dark median stripe. Femur III with 4-7 spines. Tibia II with 10-15 prolateral spines and 6-10 ventral spines.

FEMALE: Length 14-27 mm. The pattern is variable. Anterior median eyes are larger than posterior median with an equal space between eyes. The clypeus is wide, twice the diameter of an anterior median eye. The scape length is 3·0-4·10 (average 3·6 mm). There are 5-7 spines on proventral femur II. Epigynum (Figs. 14, 15); see also Dondale (1966, fig. 2E).

Apart from the presence of the second posterior tubercle on the abdomen in *E. biapicata,* the females of both species are very similar though the scape of *E. biapicata* tends to be shorter, femur II has more proventral spines, and the clypeus is



FIGS. 9–13: ♂ *Eriophora biapicata* (QM S361). 9, abdomen, lateral; 10, cephalothorax, ventral; 11, l. tibia II, prolatero-ventral; 12, l. palp, dorsoprolateral; 13, palp, mesal.
FIGS. 14–15: ♀ *Eriophora biapicata* (QM S364). 14, epigyne, posterior; 15, epigyne, lateral.

wider than in *E. transmarina*. The males of *E. biapicata* are separated on the presence of the spur on coxa II and the absence of the 4 heavy thorn-like spines on the ventral surface of femur III.

DISTRIBUTION

E. biapicata is found in Victoria, South Australia, Central Australia, West Australia and in areas west of the Great Dividing Range in New South Wales and Queensland. Occasionally a spider, probably transported by vehicles, has been found in more eastern areas of Queensland (Fig. 16). In Sydney, N.S.W., female *E. biapicata* were found in several localities. Neither *E. biapicata* nor *E. transmarina* has been found in Tasmania (Hickman, pers. comm.). *Araneus brouni* from New Zealand has a short epigyne and is distinct from these species.

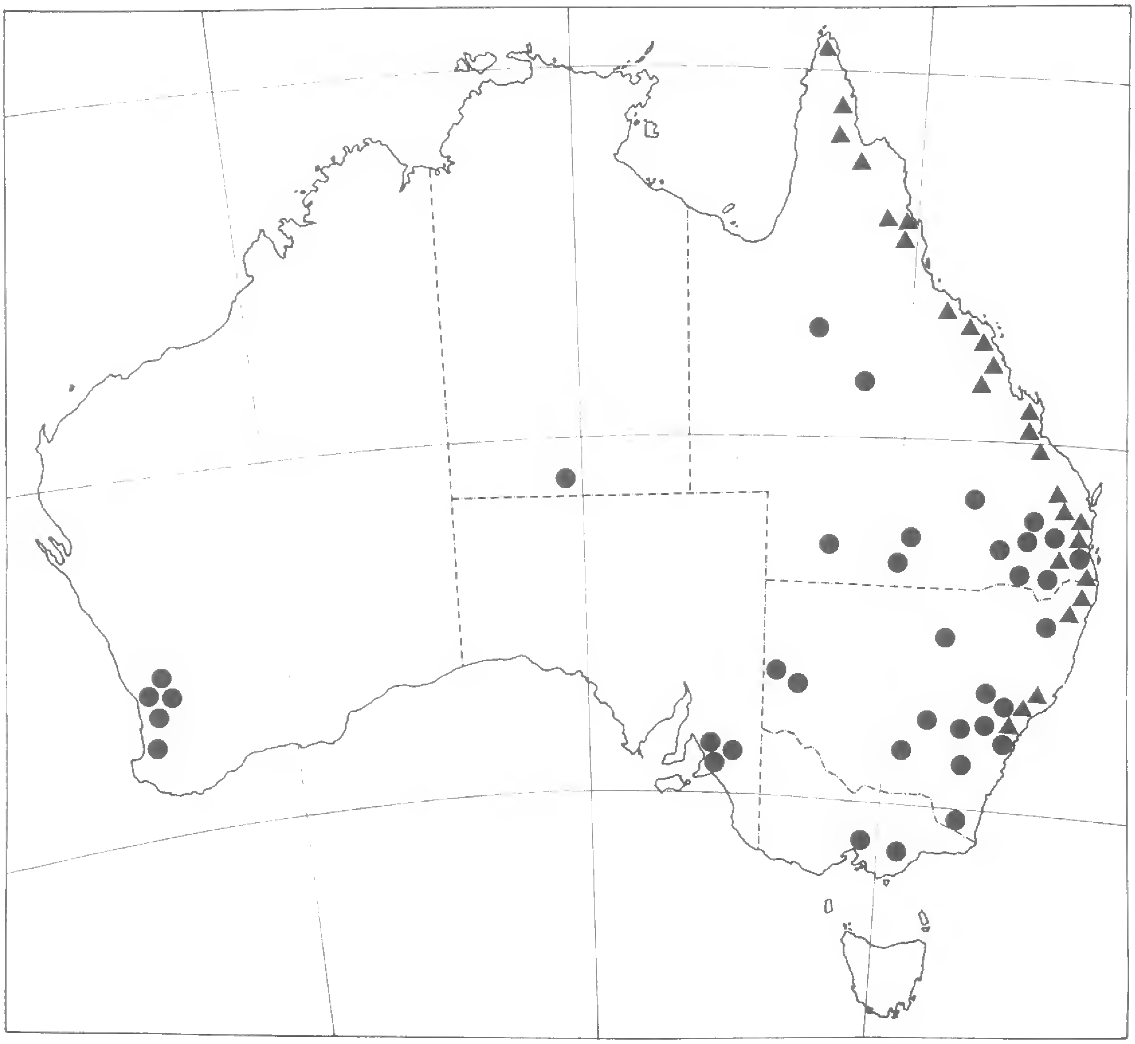


FIG. 16: Map showing distribution of *E. transmarina* (▲) and *E. biapicata* (•).

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PLATE 1

Eriophora transmarina

A: ♀ in web, feeding
B: ♂ (QM S360), 1. palp, mesal; marker = 80 μ


A

Mem. Qd Mus. **20**(1): 135–41, pl. 1 [1980].

MEGADOLOMEDES NOV. GEN. (ARANEAE: PISAURIDAE) WITH A DESCRIPTION OF THE MALE OF THE TYPE-SPECIES, *DOLOMEDES AUSTRALIANUS* KOCH 1865

VALERIE TODD DAVIES
and
ROBERT J. RAVEN
Queensland Museum

ABSTRACT

Males of this east Australian water spider are described for the first time. They show differences from *Dolomedes* which warrant the establishment of a new genus, *Megadolomedes*. *Megadolomedes* has very long legs with long, flexible tarsi. The male is very much smaller than the female and the palpal organ differs essentially from that of *Dolomedes* in having a well developed club-shaped apophysis at the base of the fulcrum. The epigyne and variations of pattern in the female are illustrated and some notes on the biology given.

Dolomedes australianus Koch 1865, *D. cervinus* Koch 1876, and *D. trux* Lamb 1911 are considered synonyms of *Megadolomedes australianus*.

Dolomedes australianus was described by Koch (1865) from an immature female from New South Wales. Later (1876) he described the mature female. The spider is found along the waterways of the east coast of Australia from Tasmania to Cape York and has been collected on Prince Edward Island in Torres Strait. The females are large spiders with body lengths varying from 20 to 30 mm and with leg spans up to 150 mm or more. The male is very much smaller with a leg span of less than 60 mm. Because of its long legs and flexible tarsi the spider bears a striking superficial resemblance to the Neotropical genus, *Trechalea*. Measurements were made with an ocular micrometer and converted to millimetres.

Abbreviations: AM, Australian Museum, Sydney; HZMI, Zoologisches Staatinstitut und Zoologisches Museum, Hamburg; QM, Queensland Museum, Brisbane. AME, ALE, PME, PLE, anterior median, anterior lateral, posterior median, posterior lateral eyes; MOQ, median ocular quadrangle.

Megadolomedes nov. gen.

Large spiders with long legs and flexible tarsi only a little shorter than metatarsi. Eyes in two recurved rows, anterior row much narrower than posterior, AME slightly larger than ALE. Retromargin of cheliceral furrow with 4 large, subequal teeth; promargin with 3 teeth, distal minute, middle largest, proximal intermediate in size. 7 spines on dorsal femur of pedipalp. Legs 4(12) 3. Superior lorum of pedicel composed of 4 sclerites, 2 median and 2 lateral. Male much smaller than female, with short palpal tibia bearing medial retrolateral apophysis. Cymbium long and slender with non-excavated distal region. Embolus very long; fulcrum well developed with a flat club-shaped apophysis basally.

Megadolomedes can be distinguished from *Dolomedes* by the characters listed in Table 1.

TYPE-SPECIES: *Dolomedes australianus* Koch 1865, the only species known for this genus.

TABLE 1: DIFFERENCES BETWEEN *MEGADOLOMEDES* AND *DOLOMEDES*.

	Megadolomedes	*Dolomedes*
tarsi	flexible; more than ⅔ length of metatarsi	not flexible; barely ½ length metatarsi
male	much smaller than ♀	about the same size, slightly smaller
cymbium	long, slender; excavated proximally, flat distally	excavated for most of length; conical distally
lateral sub-terminal apophysis	flat and club-shaped	absent

Megadolomedes australianus (Koch)

Dolomedes australianus Koch, 1865, p. 863; 1876, p. 873.
Dolomedes cervinus Koch, 1876, p. 872.
Dolomedes trux Lamb, 1911, p. 173. Rainbow, 1912, p. 210.

Material Examined

Cedar Creek Falls, Mt Nebo, near Brisbane, SE.Q., R. Raven, 16.xi.1973, 1 ♂, QM S230; Home Rule, near Helenvale, NE.Q., V. Davies, D. Joffe, 19.xi.1974, 2 ♂, QM S231; *Dolomedes australianus,* id. L. Koch, 1876, Wollongong, N.S.W., 1 ♀, HZMI, Mus. Godeffroy 302; *Dolomedes trux,* holotype, Ithaca Creek, Brisbane, SE.Q., J. Lamb, 1 penultimate ♀, QM G55; *Dolomedes trux* id. W.J. Rainbow 1912, Blackall Ranges, SE.Q., C.J. Wild, 1 juvenile, QM W2146; Pennant Hills, N.S.W., 10.viii.1953, 1 penultimate ♀, AM; Richmond Range, N.S.W., R. Raven, 14.ix.1974, 1 penultimate ♀, QM S232, Home Rule, NE.Q., V. Davies, D. Joffe, 18.xi.1974, 1 ♀, QM S233, ibid., 19.xi.1974, 2 ♀, QM S234; Davies Creek, Mareeba, NE.Q., N.C. Coleman, 30.iii.1975, 1 ♀, QM S235; Mount Molloy, N.E.Q., F. Little, ix.1969, 1 ♀, QM S236; Booloomba, Kenilworth State Forest, SE.Q., R. Raven, ii.1973, 2 ♀, QM S237; Kondalilla National Park, SE.Q., R. Raven, 10.xii.1973, 2 ♀, QM S238; Goodna reach, Brisbane River, SE.Q., R. Monroe, 13.v.75, 1 ♀, QM S239; Beerburrum, SE.Q., G.J. Male, 1 ♀, QM S240; Little Yabba Creek, Kenilworth State Forest, SE.Q., G. May, 1 ♀, QM S241; East branch Kilcoy Creek, SE.Q., K.R. McDonald, 1 ♀, QM S242; Scrubby Creek, near Eden, N.S.W., 13.xii.1971, 1 ♀, AM.

Description

Male (QM S230): Carapace length 4·48, width 3·68. Abdomen length 4·20, width 2·28. Legs 4(12)3 (Table 2). Colour (in alcohol) of carapace, legs and chelicerae yellow brown. Dorsal abdomen light brown with anterior median brown rectangular marking to about half the length of the abdomen, irregular darker areas behind. Carapace lightly covered with short brown simple hairs. Fovea length 0·25 × length of carapace, lateral striae present. Clypeus twice the longest diameter of an anterior median eye (Fig. 1). Ratio of eyes AME:ALE:PME:PLE is 8:7:14:15. MOQ width at front: width at back: length is 21:35:33. Maxillae longer than wide, 35:14 and broadest distally. Labium about as long as wide 30:27 constricted at base and rounded distally. Sternum shield-shaped, as long as wide, pointed posteriorly. Tarsi very long, curved and flexible with transverse striations, no scopula (Plate 1, C). Superior claws similar with 7–8 long teeth (Plate 1, D); inferior claw smooth and short.

TABLE 2: Leg Measurements (mm) of ♂ *Megadolomedes australianus*

	I	II	III	IV	Palp
Femur	6·13	6·44	5·44	7·00	2·63
Patella	1·88	2·19	1·75	1·94	0·88
Tibia	5·94	5·94	4·38	5·94	0·88
Metatarsus	6·25	5·88	4·75	6·88	—
Tarsus	5·13	4·83	3·50	5·13	3·75
Total	25·33	25·28	19·82	26·89	8·14

Notation of spines, First leg: Femur, p.1.1.1.1.1.d.1.0.1.0.1.r.1.1.1.1.1. Patella, p.1. d.1.r.1. Tibia, p.0.1.0.1.d.0.1.0.1.r.0.1.0.1.v.2.2. 2.2. Metatarsus, p.1.1.1.r.1.1.1.v.2.2.3. Tarsus, 0. Second leg: Femur, p.1.1.1.1.1.d.1.0.1.0.1. r.1.1.1.1.1. Patella, p.1.d.1.r.1. Tibia, p.0.1.0. 1.d.1.0.0.1.r.0.0.1.1.v.2.2.2.2. Metatarsus, p.1.1. 1.r.1.1.1.v.2.2.3. Tarsus, 0. Third leg: Femur, p.1.1.1.1.1.d.1.0.1.0.1.r.1.1.1.1.1. Patella, p.1. d.1.r.1. Tibia, p.0.1.1.d.1.0.1.r.0.1.1.v.2.2.2. Metatarsus, p.1.1.1.r.1.1.1.v.2.2.3. Tarsus, 0. Fourth leg: Femur, p.1.1.1.1.1.d.1.0.1.0.1.r. 0.0.1.1.1. Patella, p.1.d.1.r.1. Tibia, p.0.1.1. d.1.0.1.r.0.1.1.v.2.2.2. Metatarsus, p.1.1.1.r.1.1. 1.v.1.1.1.1.1.3. Tarsus, 0. Palp: Femur, p.0.0.1. 0.d.1.1.1.2.r.0.0.1.0. Patella, p.1.d.1.r.1.

Trichobothria are present in an irregular line of 11–13 running the full length of prolateral femora i–iv; some on proximal femora i–iv; some on the prolateral, dorsal and retrolateral surfaces of tibiae i–iv (most numerous proximally); 6–7 on dorsal metatarsi; and 5–6 in a single row and an additional 3–4 distally on tarsi i–iv.

Palp (Figs. 2, 3, Plate 1, B) has a slender, elongate cymbium, not excavated distally. Embolus long and whip-like, supported by the fulcrum distally. The membraneous conductor tapers to a tongue which supports the tips of the fulcrum and embolus. The median apophysis arises from the tegulum and is rounded and membraneous distally. From the base of the fulcrum a flat club-shaped apophysis, Comstock's (1948) 'lateral sub-terminal apophysis', extends posteriorly and lies against the tegulum; near its point of attachment it has a needle-like projection. A similar sharp projection arises near the base of the embolus. The tibial apophysis is a stout, curved, retrolateral spur arising mid-way along the short tibia.

Variation: The body lengths of 2 other males were 7·3 and 7·8 respectively. There is little variation in pattern and spination.

FEMALE (Plate 1, A): In 1876 Koch described *Dolomedes cerinus* which, from the description, is certainly an immature female *Megadolomedes australianus*. Lamb (1911) described *D. trux* the curved flexible nature of the tarsi is not clearly from Brisbane; on examination this is found to be a penultimate female *M. australianus*. An immature specimen QM W2146 from the Blackall Range described by Rainbow (1912) as *D. trux* is also *M. australianus*. There is great variability in size and pattern in females as noted by Koch; the spider is figured in Koch (1876, LXXV, 2) though shown. The superior lorum of the pedicel is

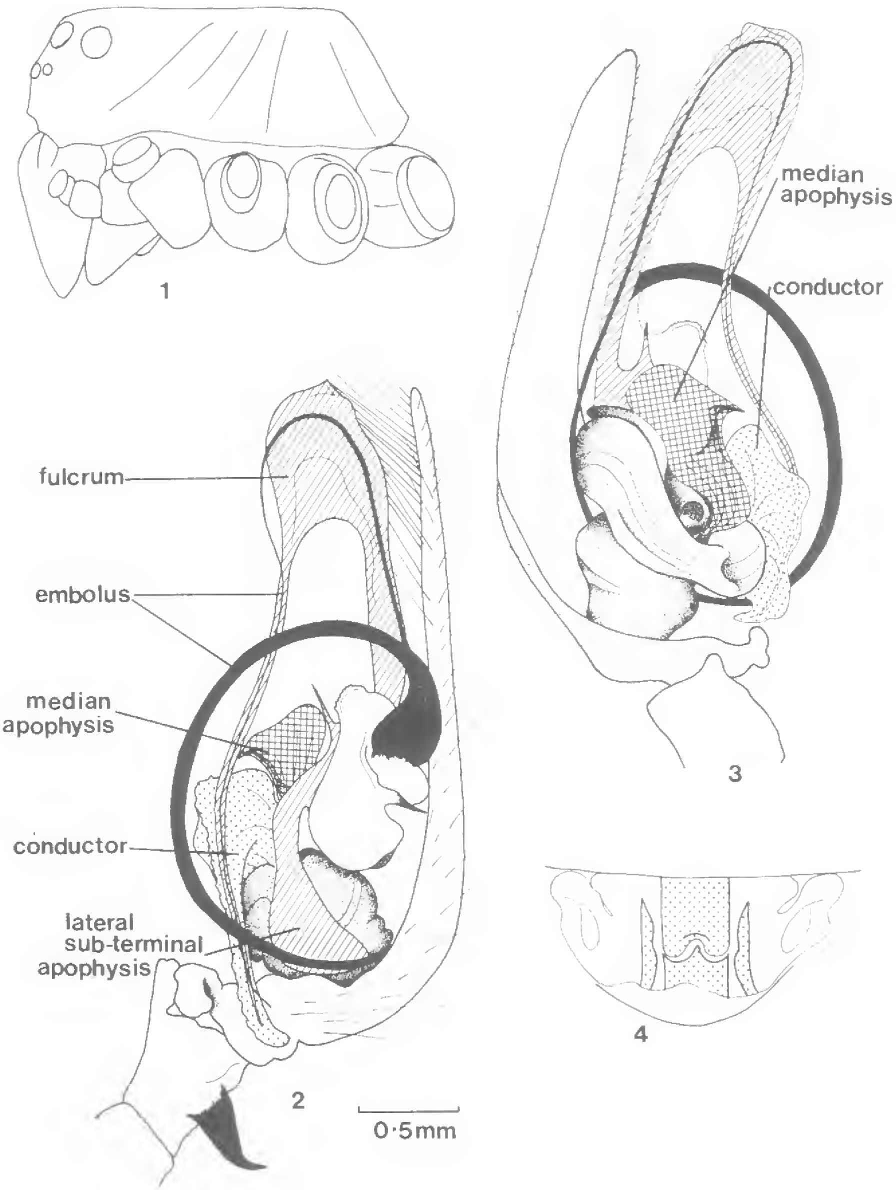

FIG. 1–4: ♂ *M. australianus*. 1, cephalothorax, lateral; 2, palp, retrolateral; 3, palp, prolateral; 4, pedicel with sclerites.

composed of 4 sclerites (Fig. 4). A scopula is present on metatarsi and tarsi of all legs. Epigynum (Figs. 5, 6) has well defined lateral ridges. The long emboli are often found blocking the epigynal ducts of the female (Fig. 7); this gives the epigynum a broader outline than usual. The atrium leads into a long twice-coiled bursa copulatrix to the ovoid spermatheca. From here a thicker, coiled fertilization tube goes to the oviduct.

Variation: Females vary in length from 20 to 30 mm. Five colour patterns may be recognised: 1) The 'type pattern as illustrated by Koch — light yellowish lateral bands on the carapace and primarily a dark foliate pattern on the dorsal abdomen. 2) The 'uniform' pattern as illustrated by Koch for *D. cervinus* — lateral cephalic bands poorly defined, if present; irregular pigmentation on the abdomen. 3) The 'spotted' pattern — carapace and abdomen brown-black marked with yellow spots. 4) The 'striped' pattern — lateral cephalic bands well defined and dorsal abdomen with a median broad dark band enclosed laterally by yellowish stripes. 5) As in Plate 1, D with more

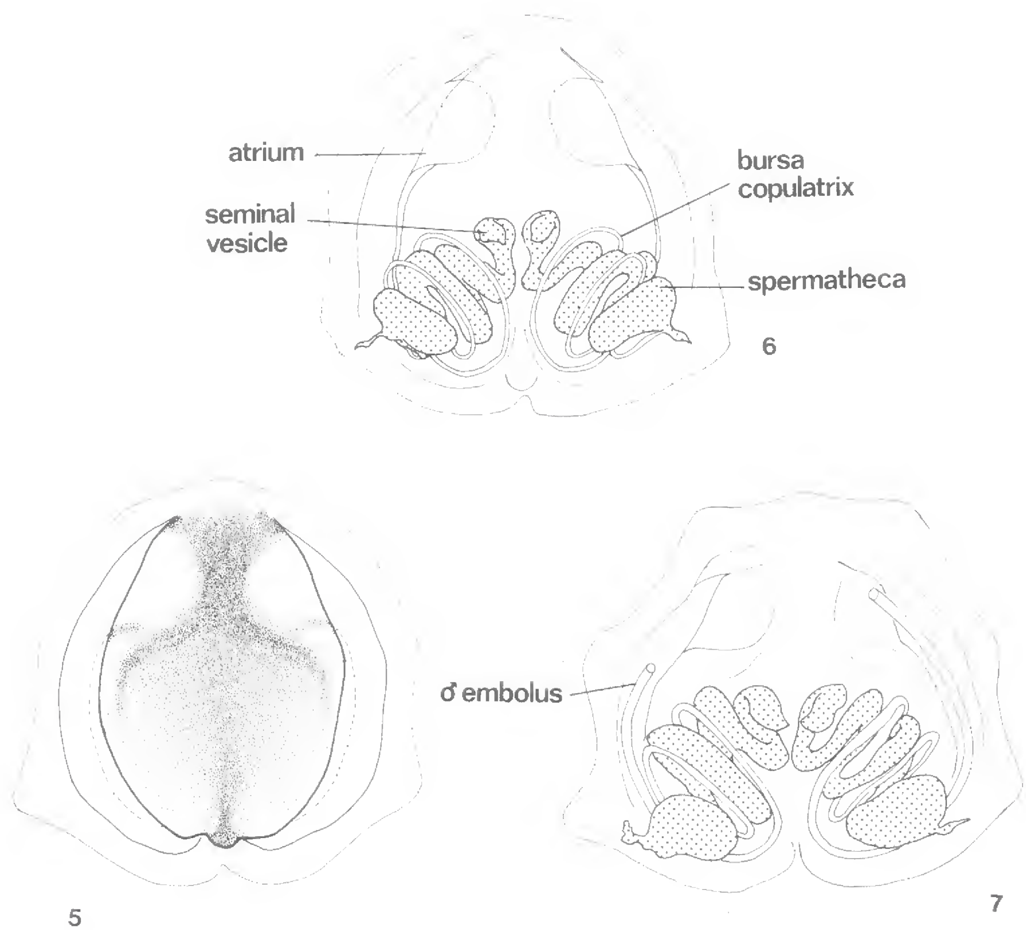

FIG. 5–7: ♀♀ *M. australianus*. 5, external epigynum S233; 6, internal epigynum S233; 7, internal epigynum with emboli in ducts S234.

extensive light areas than in 1). (Figs. 8–12). The presence of two or more patterns occurring together suggests that the patterns are of no ecological significance.

BIOLOGY

Megadolomedes australianus has a round seamless egg-sac which it carries in the chelicerae, with the aid of the palps. Just prior to the emergence of the young the egg-sac is suspended in a loosely constructed nursery in a shrub near the water (Hickman 1967). In the laboratory the young emerged from this 5–6 days later. Females are found throughout the late spring, summer and autumn in areas of still to moderately fast moving water. Males have been found only in early summer (November, December) although penultimate males were found as early as August. Before maturity they are often found high up in vegetation overhanging water. Females show a preference for the underside of logs and branches and flatten themselves if disturbed or they may dive into the water and remain submerged for nearly half an hour (Hickman 1967). In swimming the spider sculls with the second and third pairs of legs while the first and fourth pairs are held outstretched with tips together. In pursuit of prey, females strike the water with all the legs at once, thus bouncing across the water surface. The long flexible tarsi appear to be an adaptation to support the large body on water.

ACKNOWLEDGEMENTS

We should like to thank Dr Gisela Rack who gave the senior author generous access to the collections in the Zoologisches Staatinstitut und Zoologisches Museum during a visit in 1977. Thanks are also due to the Trustees of C.S.I.R.O. Endowment Fund, Canberra for financial support to travel to Europe and to the Interim Council of Australian Biological Resources Study which funded the collecting trip to northeastern Queensland during which specimens of *M. australianus* were collected.

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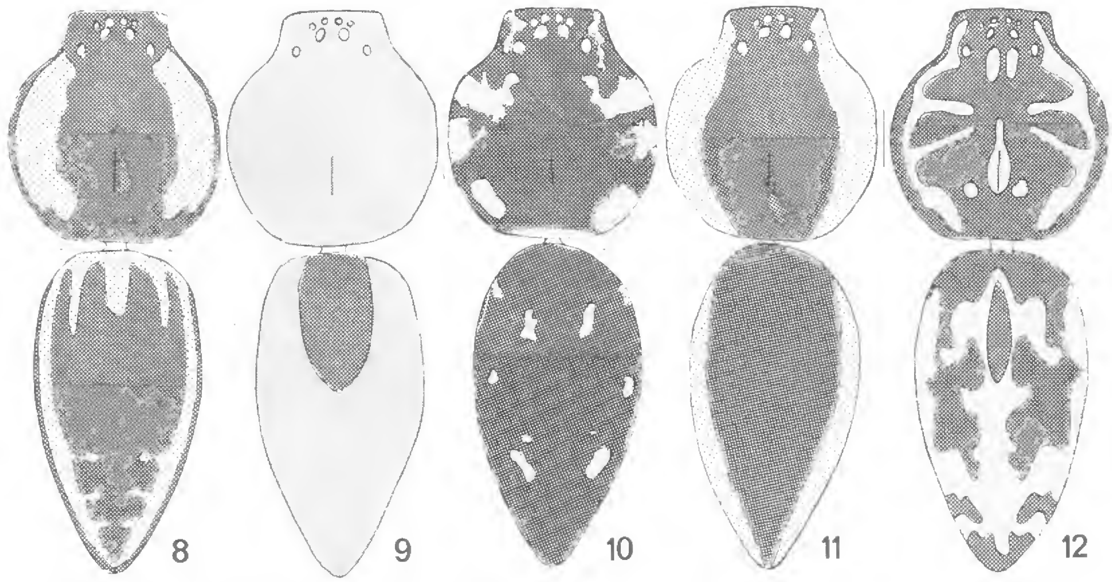
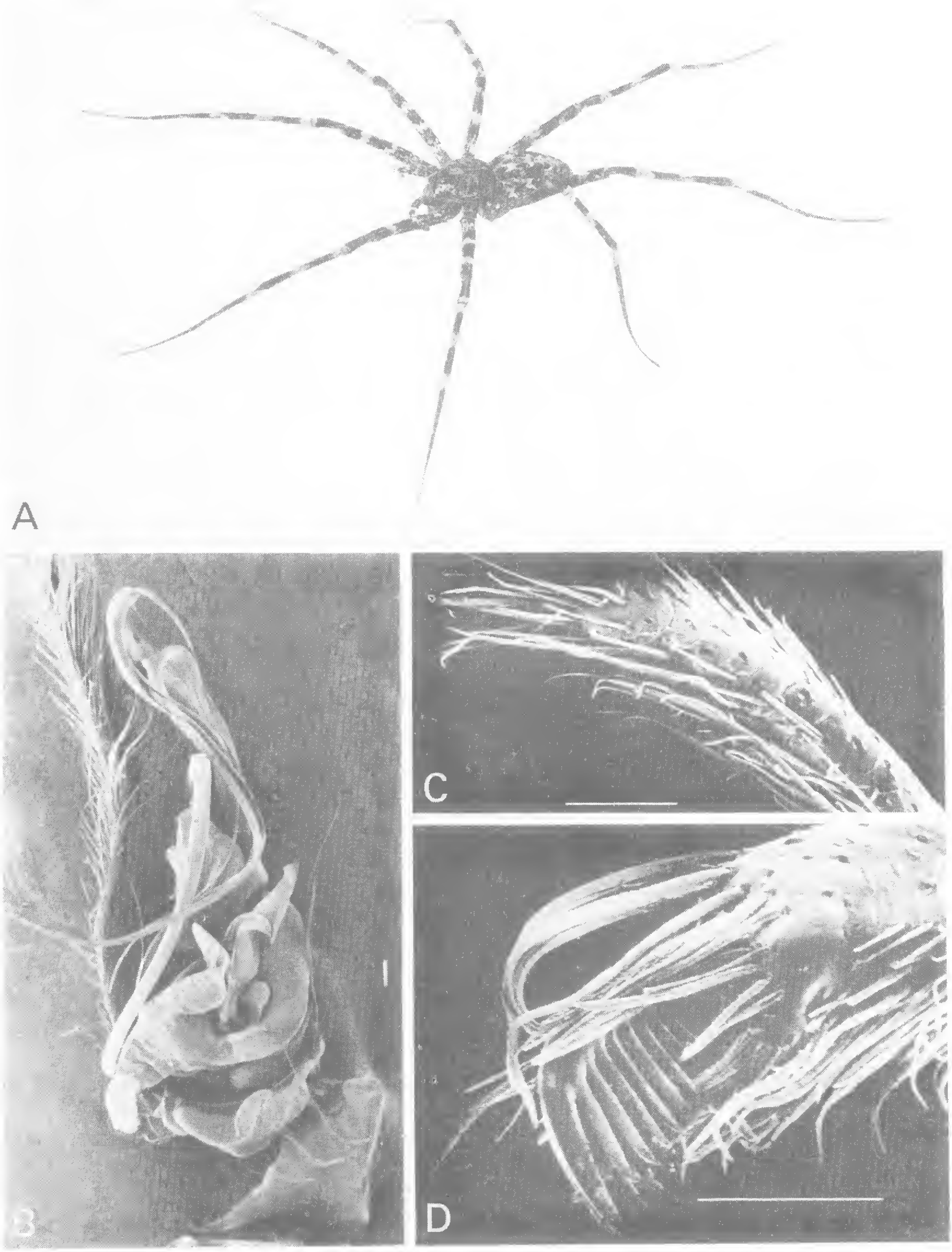


FIG. 8–12: ♀♀ *M. australianus* patterns.

PLATE 1

A: ♀ *M. australianus.*

B–D: ♂ *M. australianus.* B, palp, ventral; C, tarsus showing striations; D, tarsal claws. (Marker = 110 μ)


A
B
C
D

Mem. Qd Mus. **20**(1): 143–61, [1980].

THE ESTUARINE MACROBENTHOS OF THE CALLIOPE RIVER AND AUCKLAND CREEK, QUEENSLAND

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ABSTRACT

Quantitative benthic sampling in the Calliope River and Auckland Creek has been conducted at approximately 3 monthly intervals since November 1974 at 11 transects, each with 5 stations (55 sites). In September 1976 power generation commenced, using the estuary for thermal discharge. The data to August 1976 — the 'pre-thermal' situation — are intended to serve as the baseline for comparison with the 'post-thermal' situation. The 'pre-thermal' data are analysed here. A total of 263 taxa were found comprising 15 species of seagrasses and algae, 75 species of polychaetes, 51 species of molluscs, 91 species of crustaceans and 30 species belonging to other phyla. Of these species, those represented by less than 5 individuals, and those occurring in less than 2 sites or times, were not considered further. The remaining 72 species (representing 88.7% of all individuals collected) were classified into site-, time-, and species-groups using the 'Bray-Curtis' dissimilarily measure, followed by group-average sorting. Nine site-groups were accepted; these showed good topographic coherence and they could be characterized by their depths, substrate types, and position in the river. Classification into species-groups showed that many species were scattered throughout various sites, and on the basis of the pseudo-F test, only 39 species conformed to the site groups. Species classification using species-occurrences within the already established site-groups, gave 14 species-groups which characterize by their absence or presence, the various site-groups. Classification into time-groups showed that intertime dissimilarities are high, indicating that either sampling times were too distantly spaced, or alternately that seasonal differences overlie a non-seasonal trend. Cyclical analysis of summated species data identified a non-cyclic and a cyclic component with a period of approximately 12 months. A recolonization model has been proposed to describe these data; it is postulated that the intense flooding of December/January 1974 led to the removal of the benthos and that species reappearance was more or less linear over a period of 29 months, while the number of individuals of all species increased logarithmically. When comparisons with the 'post-thermal' fauna are made, it will be essential to allow for this recovery when assessing the thermal effects.

The utilization of estuaries as heat-sinks for electricity generating plants has stimulated considerable overseas interest in the effects of elevated temperatures on estuarine biotas (Naylor 1965, Thorhaug et al. 1973, Young and Frame 1976). In Queensland, several estuaries are affected by thermal discharges (e.g. Brisbane R., Burrum R., Ross R.) but there are no studies on the effects of elevated temperatures on estuarine biotas. As part of a general investigation into the benthic organisms of Port Curtis, the Calliope River and Auckland Creek are under study. The investigation of the macrobenthos of Port Curtis has now been terminated and an account of these data has been given (Stephenson et al. 1979).

Quantitative benthic sampling in the Calliope River and Auckland Creek has been conducted at approximately 3 monthly intervals since November 1974 at 11 transects, each with 5 stations (55 sites). With power generation commencing in September 1976, the results obtained from November 1974 to August 1976 — the 'pre-thermal' situation — are intended to constitute the baseline for comparison with the 'post-thermal' situation, and an analysis of these 'pre-thermal' results is given below.

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THE STUDY AREA

The study area (Fig. 1) comprises the Calliope River and Auckland Creek, both of which flow into Port Curtis, a semi-enclosed bay whose outer barrier consists of Facing and Curtis Islands.

Climatically, the area is sub-tropical with a mean annual rainfall of 944 mm, of which approximately 50% falls from December to February. Rainfall data, together with other meteorological and hydrological data are summarized in Table 1. Temperature, salinity and dissolved oxygen data for the Calliope River opposite the power station has been compiled from

TABLE 1: MEAN MONTHLY METEOROLOGICAL AND HYDROLOGICAL DATA FOR GLADSTONE AND CALLIOPE RIVER

Month	Mean Daily Temperature* (°C) Min/Max	Rainfall/Raindays* (mm)	Evaporation* (mm)	Humidity* (%) 9 a.m./3 p.m.	Radiation** ($MJ/m^2/day$)	Mean River Discharge*** (megalitres)
January	31·1/22·2	190/20	206	70/63	24·7	21,695
February	30·9/22·0	153/15	172	71/63	23·5	68,342
March	30·1/21·1	90/10	177	71/61	20·9	48,479
April	28·5/19·3	35/ 7	150	69/59	19·2	6,480
May	25·5/16·4	50/ 5	114	70/57	15·8	6,964
June	23·2/14·2	40/ 6	96	69/55	14·4	4,666
July	22·6/12·9	37/ 7	102	66/51	15·4	5,537
August	24·1/14·1	33/ 7	113	67/53	17·5	2,009
September	26·4/16·1	21/ 5	149	62/55	21·8	726
October	28·7/18·6	63/ 6	183	61/58	23·4	2,009
November	30·2/20·4	82/11	189	63/61	25·5	778
December	30·9/21·5	150/ 9	202	66/62	24·5	18,213
Annual	27·7/18·2	944/108	1855	67/58	20·5	185,718

* Supplied by Bureau of Meteorology
** from Paltridge and Proctor (1976)
*** Supplied by Water Resources Council of Queensland from 'Castlehope', 33 km upstream of mouth.

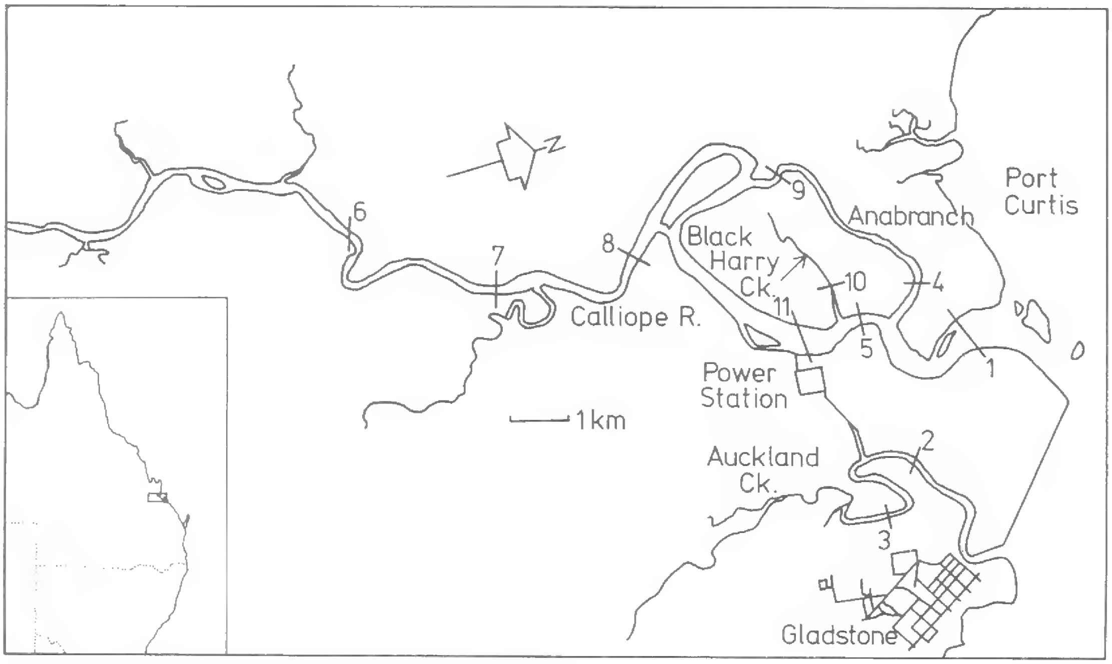

FIG. 1: Map of Study area showing locations of transects 1–11

various sources for the duration of the study period, and these are presented in Fig. 2. These data show cyclic changes in water temperature with an optimal wavelength of 12 months (Saenger et al. 1979), and somewhat less regular changes in salinity and oxygen saturations. A correlation between sharp changes in salinity and dissolved oxygen are also apparent, and the inflow of water rich in detritus is probably involved.

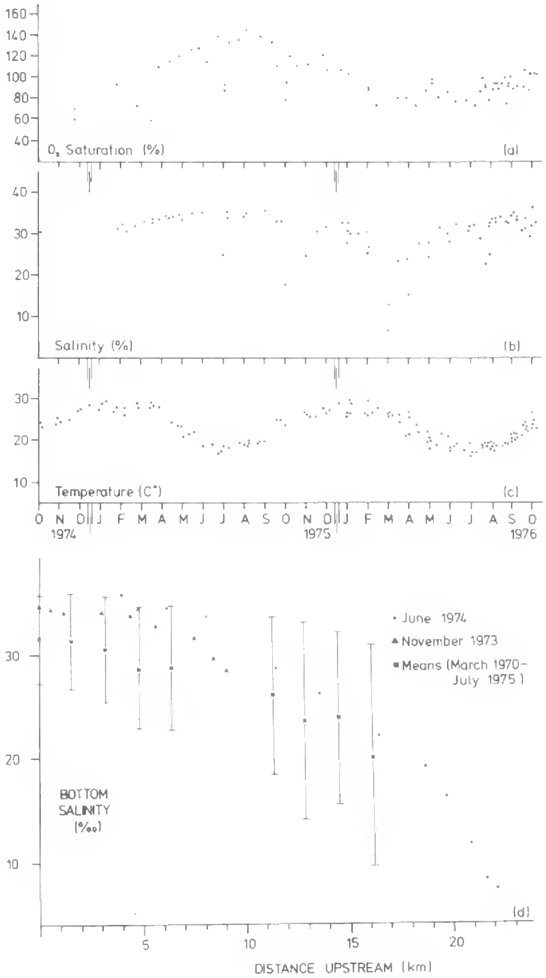

FIG. 2: Physico-chemical parameters of Calliope River; (a) oxygen saturation opposite power station site; (b) salinity opposite power station site; (c) bottom water temperatures from throughout the Calliope River; (d) decreasing salinity in the Calliope River with increasing distance upstream. (Based on data collected (i) by spot readings in the river, (ii) continuous salinity/temperature recorders, (iii) Dr J. Greenwood and (iv) Water Quality Council quarterly surveys).

The bottom sediments of the Calliope River include up to 1·3 m of mud, which covers rock, or overlies sand. The mud generally consists of soft, dark-brown or blue-grey, usually organic, silty clay (Hofmann 1971). The sand is brown to grey, silty, fine to medium grained although occasional coarse deposits are found. Gravel and shell debris occur locally, generally in the deeper channels of the river. The present day stream sediment load of the Calliope River, which drains a hinterland of argillaceous rock (Jardine 1925), is predominantly mud.

Quaternary intertidal mud deposits (predominantly quartzite and albite) overlie most of the Palaeozoic rocks to the east, north and west of the power station site (Hofmann 1971). The dark-grey to black organic mud includes layers of silt and sand. The bottom sediments of Auckland Creek include sandy clay, silty sand, and gravels in the deeper channels. Auckland Creek does not have an appreciable catchment area or stream sediment load (Hofmann 1971).

Conaghan (1966), who studied the sedimentary processes in Port Curtis, concluded that tidal circulation dominates the hydrographic features of the area. The scouring effects of tidal currents (the tidal range is up to 4·2 m), particularly at ebb tide, maintains a relatively stable balance between deposition and erosion in all tidal channels, including the smaller creeks.

METHODS

SURVEY DESIGN

Eleven transects were selected on the river and creeks (Fig. 1); each transect extends across the river from about 1 m below L.W.M. at each bank. Two transects were on Auckland Creek, one in Black Harry Creek, two on the anabranch of the Calliope River and 6 were distributed along the length of the main course of the Calliope River. Selection of transects was based on their spread along the rivers and the ease with which they could be accurately relocated. Relocation errors are about ± 2 m except at transects 1 and 11, where they are approximately ± 4 m.

At each transect, five equally-spaced stations were sampled using an 0·05 m² Van Veen grab sampler; the duplicate grabs were combined to

TABLE 2: DEPTH, UPSTREAM DISTANCE AND SUBSTRATE TYPE OF INDIVIDUAL SAMPLING SITES, 1–55.

Transect No.	Station No.	Site No.	Depth at low water (m)	Distance upstream (km)	Substrate type
1	1	1	1·6	1·3	Silty sand
1	2	2	1·9	1·3	Silty sand, some clayplug
1	3	3	1·8	1·3	Silty sand, some clayplug
1	4	4	6·1	1·3	Silty sand, some clayplug
1	5	5	5·6	1·3	Silty sand
2	1	6	1·3	2·8	Sandy silt
2	2	7	2·0	2·8	Silt
2	3	8	3·7	2·8	Silt
2	4	9	2·4	2·8	Silt
2	5	10	1·0	2·8	Yellow clay
3	1	11	0·8	5·6	Coarse sand, some gravel
3	2	12	3·1	5·6	Coarse sand
3	3	13	2·8	5·6	Coarse sand
3	4	14	2·3	5·6	Coarse sand
3	5	15	1·3	5·6	Coarse gravel
4	1	16	2·3	3·8	Coarse gravel
4	2	17	5·2	3·8	Coarse gravel
4	3	18	6·6	3·8	Coarse gravel
4	4	19	7·2	3·8	Fine sand
4	5	20	4·1	3·8	Silt
5	1	21	1·3	3·6	Soft mud
5	2	22	8·3	3·6	Sandy mud
5	3	23	8·0	3·6	Muddy sand
5	4	24	8·7	3·6	Fine sand
5	5	25	9·0	3·6	Silt
6	1	26	2·1	15·1	Solt mud
6	2	27	4·1	15·1	Mud
6	3	28	3·9	15·1	Coarse gravel
6	4	29	2·1	15·1	Coarse gravel
6	5	30	1·8	15·1	Coarse gravel
7	1	31	1·5	11·1	Coarse gravel
7	2	32	2·8	11·1	Coarse gravel
7	3	33	3·7	11·1	Mud, some gravel
7	4	34	4·8	11·1	Coarse gravel
7	5	35	2·2	11·1	Soft mud
8	1	36	3·4	8·3	Silty sand
8	2	37	4·6	8·3	Silty sand
8	3	38	4·4	8·3	Silty sand
8	4	39	4·6	8·3	Silty sand
8	5	40	2·0	8·3	Soft mud
9	1	41	0·6	7·1	Silty sand
9	2	42	2·7	7·1	Silty sand
9	3	43	5·8	7·1	Silty sand
9	4	44	4·1	7·1	Mud
9	5	45	1·2	7·1	Soft mud, some detritus
10	1	46	0·7	4·6	Soft mud
10	2	47	1·3	4·6	Mud
10	3	48	2·7	4·6	Mud
10	4	49	2·3	4·6	Mud
10	5	50	0·9	4·6	Mud
11	1	51	4·4	4·6	Coarse shell material
11	2	52	3·9	4·6	Coarse sand
11	3	53	3·6	4·6	Coarse sand
11	4	54	3·1	4·6	Coarse sand
11	5	55	2·2	4·6	Coarse sand

give a total of 0·1 m² sampled at each of 55 sites in all. For each transect and station, data on depth, sediment type and distance upriver are given in Table 2.

SAMPLE TREATMENT

Sampling was carried out at approximately three-monthly intervals as follows: November 1974; March 1975; June 1975; October 1975; February 1976; May 1976 and August 1976. These times are referred to below as T_{1-7} respectively. On all occasions all sites were sampled although at some site-times, no organisms were found (Table 3).

All samples were subsequently sieved through an 8 mm (to break up the sediments) and a 1 mm sieve in the field and that fraction retained by the fine sieve was fixed in 5% formalin/seawater and subsequently transferred to glycerol: water: ethanol (5:25:70 v/v). Seagrasses and algae were blotted dry and weighed. In order to make these weights approximately equivalent to faunal numbers, the weights were multiplied by 10.

TABLE 3: SITE-TIMES AT WHICH NO ORGANISMS WERE FOUND IN THE SAMPLES

Times	Sites
1	24 28 29 30 32 34 50 55
2	11 35 46 48 54
3	9 15 21 23 24 29 49
4	49
5	45
6	—
7	—

Numerous taxonomic problems were encountered while working up the collections and the assistance of many specialists was enlisted (see acknowledgements). Once species had been identified, subsequent identifications were generally made using validated reference material, except in a few difficult groups such as some polychaetes, echinoderms and ascidians.

ANALYSES OF DATA

Initially the data were treated as three-dimensional i.e. time (1–7) × transect (1–11) × station (1–5), or as two-dimensional i.e. time (1–7) × sites (1–55). In addition there was a species dimension of 263 if all species are included. Five different sample parameters (s number of species; n number of individuals of all species; G Gleason diversity; H' standardized Shannon diversity to log base 2; J' Shannon equitability) were derived from summations involving all species, and five matrices of times × transects × stations were considered.

CLASSIFICATION

For classificatory purposes, the less abundant species — those with less than 5 individuals in the 385 samples — were eliminated. This reduced the species number to 120, and gave a basic matrix for classification of 120 species × 55 sites × 7 times. Five of these species however were subsequently eliminated because they occurred in less than 2 sites.

Classification into species-, time-, and site-groups were thus initially based on 115 species. For further time-group classification, an additional 6 species were eliminated as they occurred only once. Site classification based on 115 species suggested that many species were scattered throughout the different site-groups, and while these species may be important ones, for classificatory purposes they are in the nature of 'background noise'. These species were ignored during the final site classification, leaving a residuum of 72 species for the determination of site-groups; these 72 species represent 88.7% of all individuals collected during this study.

Data transformations were used as follows: Site classification involved use of the $\log_{10}(n+1)$ transformation followed by the 'Bray-Curtis' dissimilarity measure with subsequent group-average sorting. For species, the transformed values were standardized by totals followed by 'Bray-Curtis' dissimilarity and group-average sorting as before. Data for times were averaged over the 55 sites and transformed by $\log_{10}(n+1)$, and then classified using 'Bray-Curtis' dissimilarity and group-average sorting.

PERIODICITY

Analyses of periodicity followed the iterative technique described in Saenger et al. (1979) and Stephenson and Burgess (in press). It consists of running the generalized equation,

$$Y = \tfrac{1}{2}A^\circ + A\cos\left(\frac{2\pi t}{T}\right) + B\sin\left(\frac{2\pi t}{T}\right)$$

where Y is the recording of a species at time t,
T is the wavelength of the curve,
$\tfrac{1}{2}A^\circ$ is the estimated midpoint of the curve,
A is the contribution of the cosine component,
B is the contribution of the sine component.

through a series of wavelengths, and determining the proportion of the total sum of squares accounted for by the regression (R^2). If the selected wavelength is the predominant one in the system, then R^2 will be maximal.

TABLE 4: FAUNISTIC COMPOSITION OF THE CALLIOPE RIVER AND AUCKLAND CREEK MACROBENTHOS.

Phylum and class	Total No. individuals	No./Station	Total No. of species
Thallophyta	2·71*	49**	14
Anthophyta	7·33*	133**	1
Sub-totals	10·04*	182**	15
Coelenterata			
Anthozoa	11 (0·1%)	0·2	2 (0·8%)
Pennatulida	2 (0·1%)	0·1	2 (0·8%)
Alcyonaria	3 (0·1%)	0·1	1 (0·4%)
Nemertea	29 (0·4%)	0·5	1 (0·4%)
Echiura	9 (0·1%)	0·2	1 (0·4%)
Platyhelminthes			
Turbellaria	11 (0·1%)	0·2	2 (0·8%)
Bryozoa	4 (0·1%)	0·1	1 (0·4%)
Annelida			
Polychaeta	1455 (19·0%)	26·5	76 (30·6%)
Oligochaeta	1 (0·1%)	0·1	1 (0·4%)
Mollusca			
Pelecypoda	1927 (25·2%)	35·03	33 (13·3%)
Gastropoda	521 (6·8%)	9·47	17 (6·9%)
Scaphopoda	12 (0·2%)	0·2	1 (0·4%)
Arthropoda			
Crustacea	2150 (28·1%)	39·09	91 (36·7%)
Pycnogonidae	7 (0·1%)	0·1	3 (1·2%)
Echinodermata			
Ophiuroidea	399 (5·2%)	7·25	7 (2·8%)
Holothuroidea	1023 (13·4%)	18·6	1 (0·4%)
Phoronida	1 (0·1%)	0·1	1 (0·4%)
Chordata			
Ascidiaceae	16 (0·2%)	0·3	3 (1·2%)
Pisces	59 (0·8%)	1·07	4 (1·6%)
Sub-totals	7640	138·9	248
Total			263

* as grams
** as mg/station

TABLE 5: NUMERICALLY MOST ABUNDANT BENTHIC SPECIES.

Code No.	Species	Total No. of Individuals		% of Site-times at which species found
	POLYCHAETA		% of all polychaetes in surveys	
76	*Glycera americana*	186	12·8	27·3
86	*Leitoscoloplos* sp. nov.	54	3·7	3·6
95	*Nephtys mesobranchia*	70	4·8	9·6
98	*Ophelina* sp.	54	3·7	8·8
104	*Prionospio* sp.	58	4·0	6·2
111	*Scoloplos implex*	111	7·6	3·9
124	*Magelona dakini*	110	7·6	7·8
	CRUSTACEA		% of all crustaceans in surveys	
	BRACHYURA			
194	*Paracleistostoma mcneilli*	76	3·5	5·7
	AMPHIPODA			
238	*Dryopoides* sp.	228	10·6	8·3
239	*Ericthonius* sp.	180	8·4	3·6
242	*Grandidierella* sp. I	51	2·4	4·4
243	*Grandidierella* sp. II	143	6·7	11·4
	TANAIDACEA			
276	*Apseudes estuarius*	649	30·2	4·7
	MYSIDAE			
298	*Unident.* sp. IV	62	2·9	1·0
	ISOPODA			
302	*Sphaeroma* sp.	58	2·7	3·4
	MOLLUSCA		% of all molluscs in surveys	
	GASTROPODA			
331	*Nassarius burchardi*	335	13·6	37·4
	BIVALVIA			
356	*Circe cf. australis*	68	2·8	9·1
364	*Gouldia* sp. I	109	4·4	15·1
368	cf. *Laternula* sp.	621	25·2	20·3
371	*Modiolus auriculatus*	109	4·4	7·3
372	*Notospisula parva*	329	13·4	19·2
377	*Solecurtis* sp.	269	10·9	11·7
381	*Tellina* sp.	236	9·6	21·3
	ECHINODERMS		% of all echinoderms in survey	
	OPHIUROIDEA			
405	*Amphiura micra*	365	25·7	8·0
	HOLOTHUROIDEA			
408	*Protankyra verrilli*	1,023	71·9	23·4
	FISH		% of all fish in survey	
	PISCES			
452	*Brachyamblyopus cf. urolepis*	53	89·8	11·2

RESULTS

FAUNISTIC COMPOSITION

A total of 263 taxa were recorded in the survey although some are probably oversplit (e.g. *Magelona* and MAGELONIDAE sp. I) whilst others require subdivision (e.g. *Squilla, Alpheus*). All species are listed in the Appendix together with the code numbers used throughout.

Of the 263 taxa, 15 were seagrasses or algae (Table 4). Amongst the faunal taxa, 36.7% were crustaceans, 30.6% polychaetes, 20.6% molluscs and 12.1% belonged to other groups (Table 4). In terms of the 7640 individuals recorded, 28.1% were crustaceans, 32.2% molluscs, 19.0% polychaetes and 20.7% belonged to other groups (Table 4). The most numerous species within these categories are listed in Table 5.

Several new species have been found in this study, including the polychaete *Nephtys mesobranchia* Rainer and Hutchings (1977) and the pycnogonid *Propallene saengeri* Staples (1979). In addition, several new Australian records were established including significant extensions to the previously known ranges; these species are indicated in the Appendix.

By summating the station data for each transect in the main channel of the Calliope River, it is possible to obtain an overall view of the upstream distribution of organisms. Two trends are

apparent in this data; Fig 3a shows that the total number of species recorded at each transect decreased with increasing distance upstream. Presumably this reflects the gradual loss of marine species with increasing freshwater influence. The second trend (Fig. 3b) is in the number of organisms per m², and shows an initial decrease — minimum approximately 8 km upstream of the mouth — followed by a rapid increase upstream of this point. This upstream increase is largely due to a few species of amphipods, *Apseudes estuarius*, and the mussel *Modiolus auriculatus*, suggesting that these species reach large numbers in the presence of a marked freshwater influence.

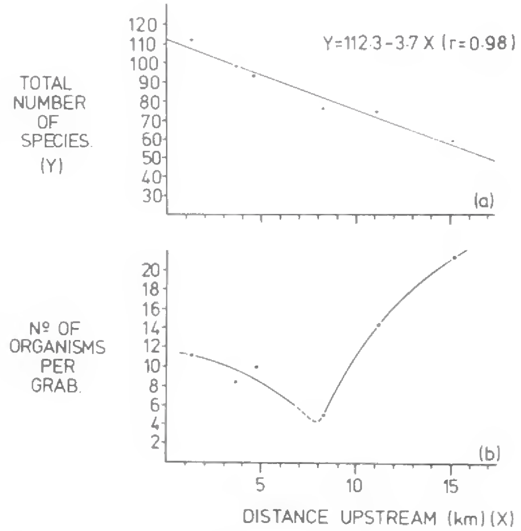

FIG 3: Upstream distribution of species and individuals of all species in the Calliope River.

MEAN SAMPLE PARAMETERS

The meaned data from various groupings of samples are given in Table 6. Overall means were: *s* 6·08; *n* 20·08; *G* 1·86; *H'* 1·76 and *J'* 0·71. From each row, the mean sum of squares (mss) was obtained (Table 6) and these indicate that there is much greater heterogeneity between times than between transects, and between transects than between stations. It is also evident that there is a hierarchy of heterogeneity between the parameters with *n*>*s*>*G*>*H'*>*J'*. The main cause of times heterogeneity is the high value of all parameters (except *J'*) at time T_7 (August 1976), contrasted with the low values in T_2 (March 1975). The likely importance of this is discussed later.

TABLE 6: MEANS OF THE 5 SAMPLE PARAMATERS (*s, n, G, H'* AND *J'* (IN THE 7 TIMES, 11 TRANSECTS AND 5 STATIONS. (ALSO MEAN SUM OF SQUARES VARIATION IN EACH ROW.)

	TIMES 1	2	3	4	5	6	7	MSS
s	3·36	2·16	4·04	5·31	4·87	7·40	15·44	16·905
n	7·56	3·78	8·25	12·04	12·47	20·05	76·38	550·662
G	1·25	0·78	1·48	1·86	1·66	2·27	3·71	0·759
H'	1·33	0·80	1·51	1·80	1·75	2·23	2·88	0·378
J'	0·69	0·51	0·68	0·77	0·78	0·80	0·77	0·009

	STATIONS 1	2	3	4	5	MSS
s	6·10	6·32	6·65	5·47	5·87	0·160
n	20·43	17·69	21·74	19·58	20·95	1·919
G	1·84	2·05	1·99	1·65	1·76	0·021
H'	1·79	1·97	1·79	1·53	1·72	0·020
J'	0·73	0·79	0·72	0·64	0·68	0·003

	TRANSECTS 1	2	3	4	5	6	7	8	9	10	11	MSS
s	7·49	6·49	6·00	7·00	7·20	5·60	5·54	4·71	6·97	3·89	6·03	1·114
n	23·66	21·23	21·54	12·74	16·94	43·20	28·86	9·77	15·57	7·83	19·51	88·059
G	2·20	1·97	1·88	2·27	2·34	1·32	1·52	1·56	2·19	1·43	1·78	0·120
H'	2·06	1·83	1·67	2·09	2·12	1·29	1·53	1·61	2·12	1·37	1·67	0·084
J'	0·78	0·75	0·73	0·81	0·77	0·51	0·64	0·69	0·81	0·66	0·68	0·007

SITE CLASSIFICATION

Classifying the 55 sites using 72 species, the sites dendrogram (Fig. 4) was resolved into 9 site-groups; their topographic coherence is shown in Fig. 5 while their depths, substrate types and their position in the river are given in Table 7.

Two site-groups (III, V) consist of a single site respectively; while site-group V is not easy to

reallocate, site-group III could be easily fused with site-group IV but it has been retained separately because of the presence of characteristically high frequencies of the isopod *Sphaeroma* and the bivalve *Circe* cf. *australis*.

Species Classification

Species classification using 115 species gave 10 species-groups which could be characterized broadly as 'widespread', 'upstream' or 'downstream'. Perusal of a two-way coincidence table of species-groups in sites showed however that many species were scattered throughout various sites

TABLE 7: Abiotic Characterization of Site-groups.

Depth	Upstream	Downstream				
	Sand/gravel	Mud	Coarse Sand	Fine Sand	Sandy Mud	Sand/Mud/ Gravel
Shallow <2 m		IX				
Intermediate 2–4 m	II	IV	V	VI	VII	
Deep >4 m		III		I		VIII

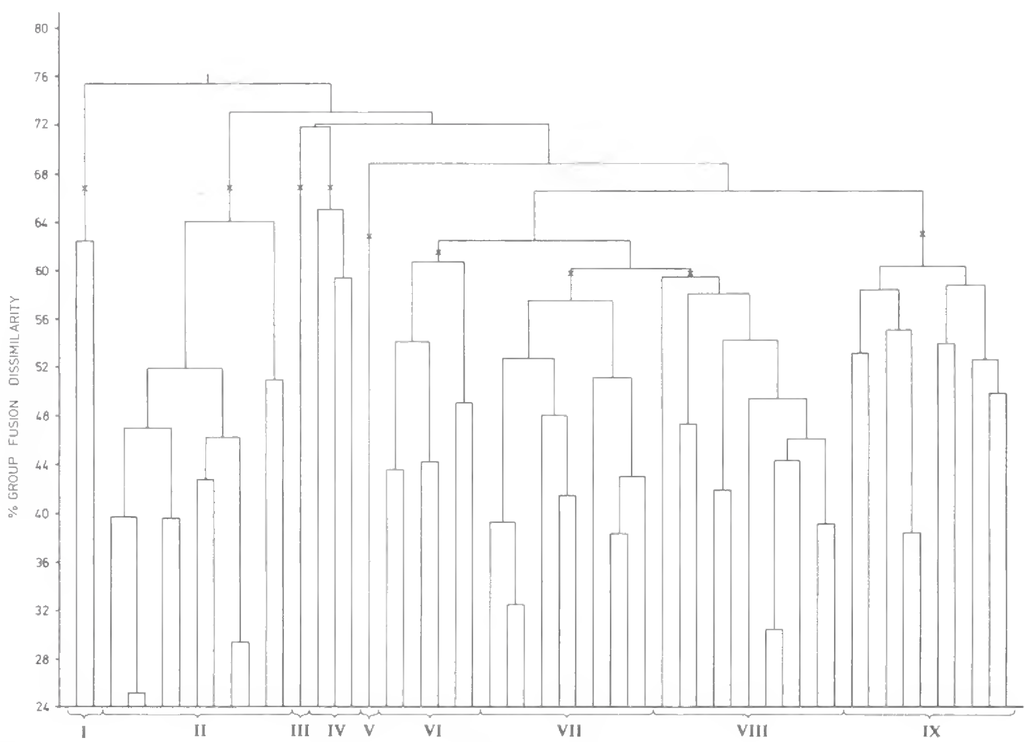

Fig. 4: Dendrogram of site-groupings using 72 species. (X) indicates site-groups accepted.

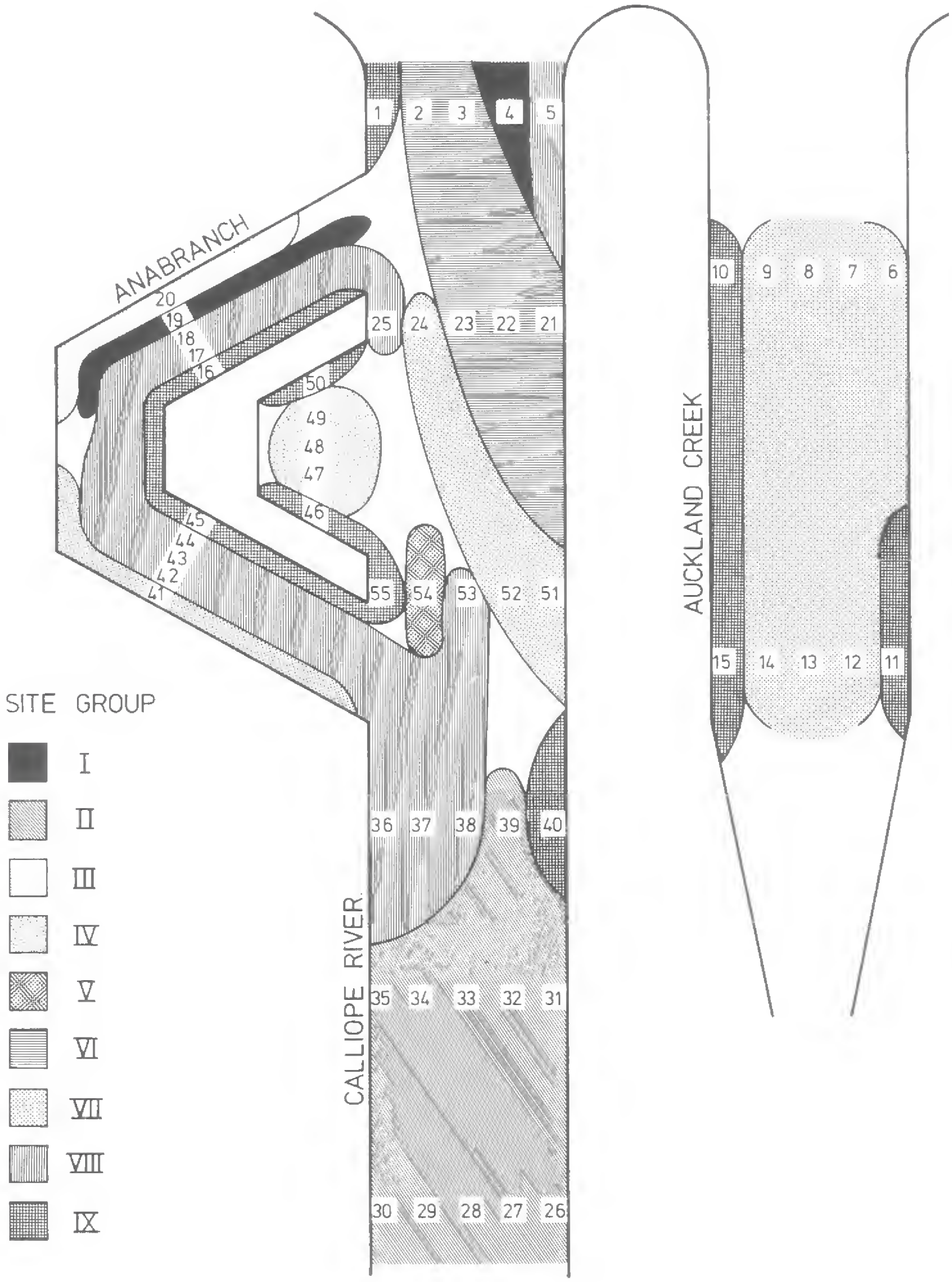

FIG. 5: Schematic representation of the distribution of site-groups I–IX together with the individual sites.

and only 39 species conformed at an equivalent to the 0·10 probability level, when using the pseudo-F test (Stephenson and Campbell 1977) with log transformed data.

Reclassification using only 72 species resulted in 18 species-groups but again, little conceptual insight was gained.

Since the site classification made good topographic and sedimentary sense, the 115 species were classified by using the species occurrences after standardization by the total number of occurrences (log transformed) within the already established site-groups. Classification of these data gave 14 species-groups (Fig. 6) which were accepted as forming more or less natural units (Table 8).

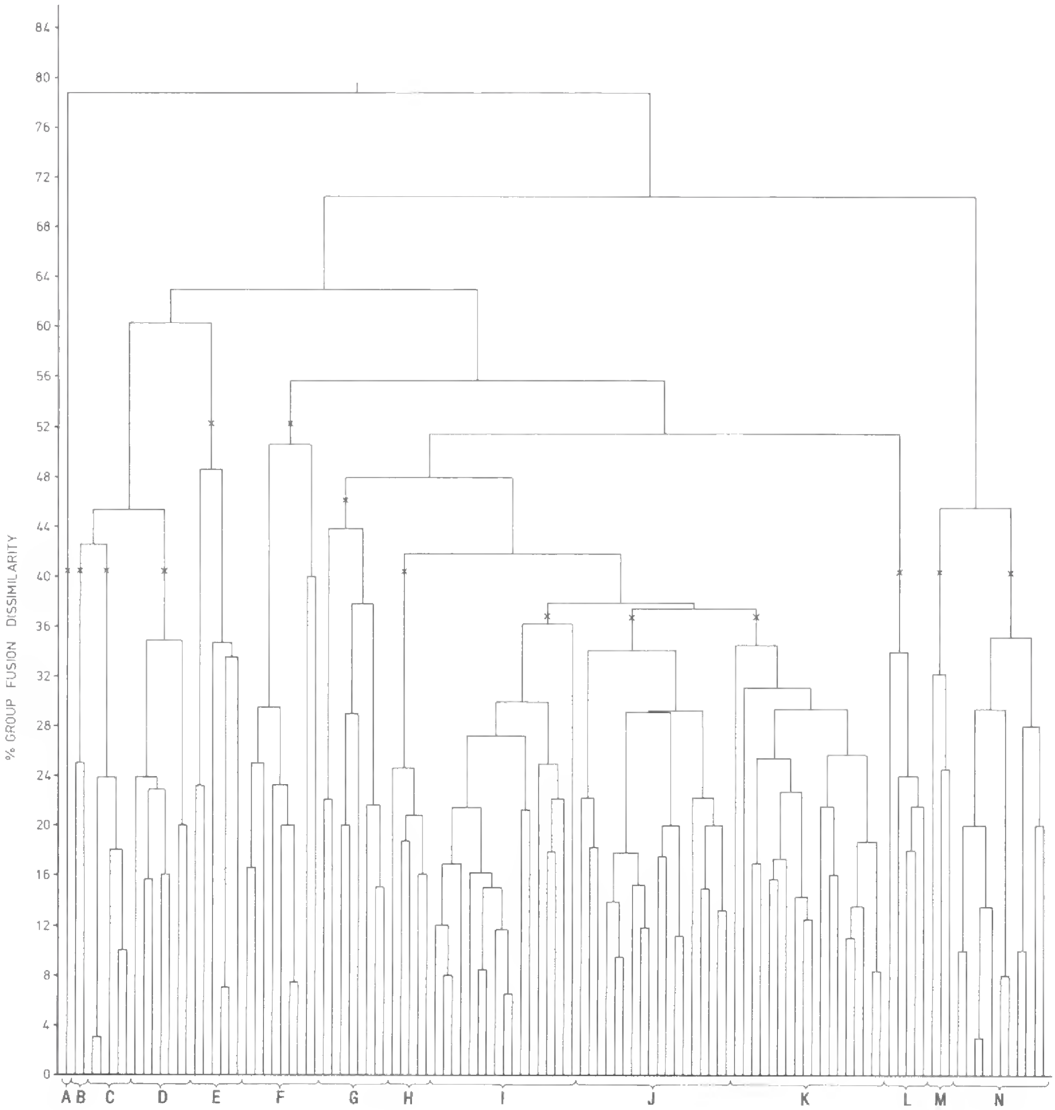

FIG. 6: Dendrogram of species-grouping using 115 species. Crosses indicate species-groups accepted. The individual species comprising these species-groups are given in Table 8.

TABLE 8: INDIVIDUAL SPECIES (BY CODE NUMBER) IN SPECIES-GROUPS A–N AS ACCEPTED IN DENDROGRAM (FIG. 6).

Species Group	Species Composition
A	427
B	197 334
C	51 88 188 327 330
D	79 86 177 187 194 229 298
E	26 69 75 90 303 311
F	67 113 114 115 136 142 156 157 277
G	102 109 122 236 295 312 332 401
H	78 100 130 134 336
I	66 87 95 124 133 140 153 238 242 243 331 368 369 372 381 403 452
J	32 46 76 82 89 91 98 104 105 151 159 206 301 333 339 364 377 408
K	77 96 119 123 160 185 244 251 281 286 287 294 352 356 365 366 380 405
L	3 234 237 378 426
M	74 302 371
N	56 85 101 111 180 183 239 241 247 276 362

TABLE 9: MEAN PERCENTAGES OF SPECIES - GROUPS IN SITE - GROUPS

Species Group	Site - group								
	I	II	III	IV	V	VI	VII	VIII	IX
A	0	0	0	0	0	0	0	**100**	0
B	0	0	0	0	**12·5**	0	0	**25·0**	**62·5**
C	0	0	0	1·8	0	10·8	**20·0**	0	**67·4**
D	0	**26·0**	6·7	2·9	0	1·3	9·4	8·0	**45·7**
E	4·5	1·7	0	**12·7**	4·2	**40·7**	5·0	0	**31·5**
F	3·9	5·1	2·8	0·7	7·9	10·4	**42·6**	1·6	**25·4**
G	6·6	3·8	3·3	3·8	0	**31·0**	**12·0**	**39·6**	0·8
H	0	10·4	0	7·0	2·4	11·6	**47·6**	**19·8**	1·0
I	2·6	**22·6**	2·6	3·5	0·4	6·9	**17·5**	**28·8**	**15·1**
J	5·6	5·9	0·8	1·3	2·4	**14·4**	**26·0**	**19·1**	**24·7**
K	6·0	4·1	1·4	0·5	0·6	**10·7**	**29·4**	**39·1**	8·4
L	**25·8**	5·0	0	0	0	**12·8**	0	**38·6**	**17·8**
M	5·0	**41·7**	6·0	6·0	0	7·7	0	**22·3**	11·3
N	0	**73·3**	0	0	0	8·2	7·1	8·3	3·2

SPECIES-GROUPS IN SITE-GROUPS

From the species and site classifications, a coincidence table was prepared using the means of species-groups proportions within site-groups (Table 9); heavy type has been used for values greater than 12%. From this table it is readily recognizable which species-groups characterize which site-groups, and which site-groups are the focus of a species-group. For example the species-groups characterizing the most upstream site-group (II) are readily apparent (species-group M and N), while Table 8 allows the individual species in these species-groups to be identified by code number.

TABLE 10: CHARACTERIZATION OF SITE-GROUPS I – IX

Site Groups	Mean Distance Upstream (km)	Predominant Substrate	Mean Depth (m)	Total No. Species	Flora (mg/m^2)	Fauna (N/m^2)	H'	G	J'	Characterizing Species-groups
I	2·6 ± 1·8	Sand	6·7 ± 0·8	59	157	92·1	2·01	2·09	0·88	(+)L (–)A,B,C,D,H,N
II	12·7 ± 2·5	Sand + Gravel	3·1 ± 1·2	99	5	332·7	1·37	1·36	0·57	(+)D,I,M,N (–)A,B,C
III	3·8	Mud	4·1	32	71	122·9	1·74	1·81	0·74	(+) nil. (–)A,B,C,E,H,L,N
IV	4·6	Mud	2·1 ± 0·7	42	152	46·2	1·15	1·24	0·59	(+)E (–)A,B,L,N
V	4·6	Gravel	3·1	27	0	118·6	1·25	1·38	0·45	(+)B (–)A,C,D,G,L,M,N
VI	3·4 ± 2·1	Sand + Mud	3·7 ± 3·5	113	955	143·1	2·06	2·28	0·79	(+)E,G,J,K,L (–)A,B
VII	4·1 + 1·3	Mud + Sand	3·5 ± 2·1	122	3	225·1	1·83	2·02	0·78	(+)C,F,G,H,I,J,K (–)A,B,L,M
VIII	5·8 ± 2·4	Sand + Mud + Gravel	5·0 ± 1·8	162	51	170·0	2·13	2·30	0·79	(+)A,B,G,H,I,J,K L,M (–)C,E
IX	4·8 ± 2·0	Mud	1·4 ± 0·6	128	713	171·1	1·71	1·71	0·70	(+)B,C,D,E,F,I,J,L (–)A

Not only positive but also negative characterizations can be seen (Table 9) and these have been used to give an overall characterization of the site-groups (Table 10).

TIMES CLASSIFICATION

Results of the times classification using 109 species are shown in Fig. 7. The times dendrogram can be accepted at either a 2-group level or a 4-group level; the former splits the early times (T_{1-5}) from later times (T_{5-7}) while the latter gives T_2, $T_{1,3,4}$, T_5 and T_{6-7}.

Species classification based on times gave 17 species-groups; most of these were sequential groups. Two species-groups emerged which were present throughout the period with the exception of the two later summer times (T_2 — March 1975 and T_5 — February 1976): Species-group A contained only one species, the bivalve *Solen correctus*; species-group B contained the following 10 species — 98, 113, 157, 187, 188, 242, 244, 330, 366 and 401.

Pseudo-F tests of conformity of species to the two levels of time-groupings were performed using a conformity level equivalent to 0·10. Sixty-two species failed to conform to either grouping, and it appears that the time-groupings are partly sequential and partly seasonal.

Intertime dissimilarities are high; the lowest is at approximately 27% while the highest fusion is at approximately 67% dissimilarity. This suggests that either times were too distantly spaced for clear trends to show in the data, or that seasonal differences overlie a non-seasonal trend. On the basis of at least two seasonal species-groups and of cyclical analyses, the latter alternative appears to be the correct one, and no further time-classifications were undertaken.

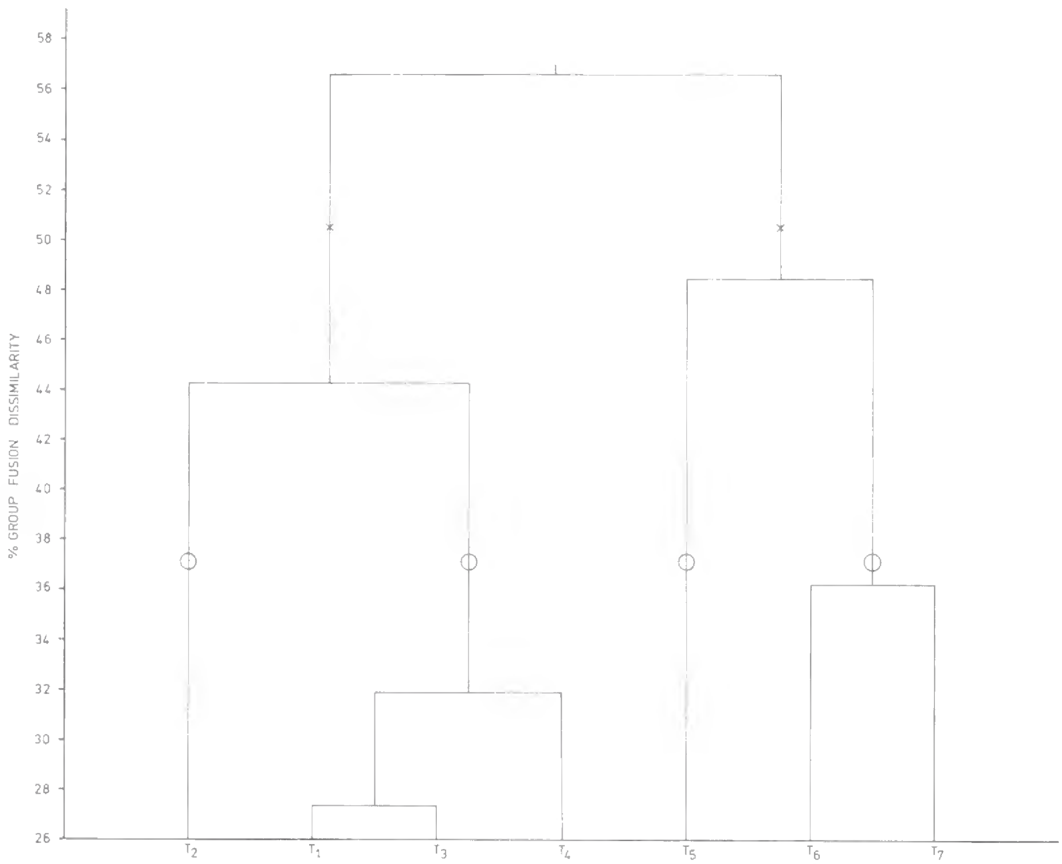

FIG. 7: Dendrogram of time-groupings using 107 species. Circles and crosses indicate the alternate 2-group or 4-group level of acceptance.

SEASONALITY

Because of the low and scattered recordings of many individual species, no attempt was made to subject individual species to cyclic analyses after non-cyclic components had been identified. However two-stage regressions were determined for the summated data.

One stage regressions were performed between times (in months) and the summated values of *s*, *n*, *H'*, *G* and *J'*. Linear, power curve fit, exponential logarithmic regressions were calculated and significant regressions are given below, and superimposed on Fig. 8.

s, linear, $s = 5{\cdot}25\ t + 28{\cdot}8$ $r^2 = 0{\cdot}80$

n, exponential, $n = 187\ e^{0.11t}$ $r^2 = 0{\cdot}76$

G, linear, $G = 0{\cdot}554\ t + 6{\cdot}70$ $r^2 = 0{\cdot}87$

It will be noted that the underlying linear trend in the number of species becomes zero at –5·5 months, or approximately April 1974, while *G* becomes zero at –12.1 months, or approximately October 1973.

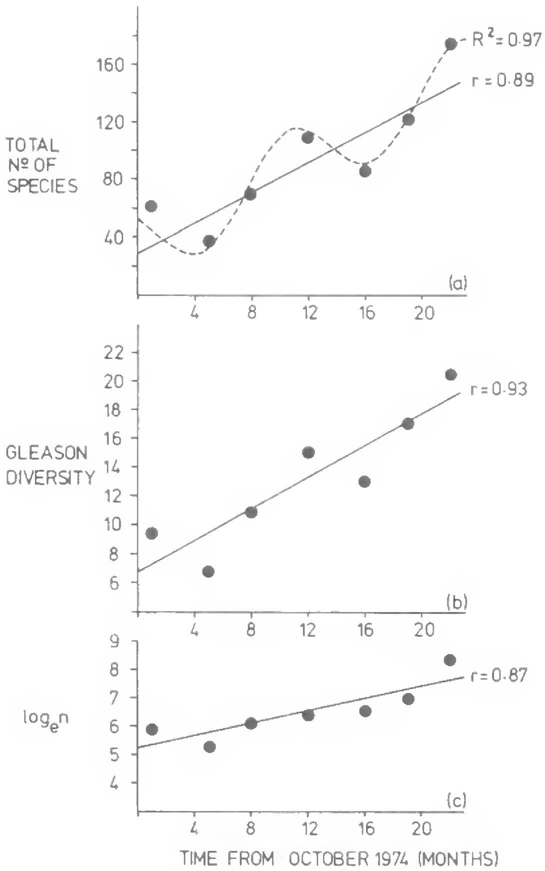

FIG. 8: Changes in parameters, *s*, *G* and *n* summated for all sites, for T_1–T_7

Having identified the non-cyclic components in the data, the residuals were examined for near-annual cycles, using cycles of 9·5 to 13 months in increments of 0·5 months. The values of R^2 (proportion of variance take up) in each case were maximal for cycles of 10·5 months. Considering the total regressions (i.e. linear/ exponential plus 10·5 month cycle), R^2 for significance at 0·05 is 0·903 and at 0·01 is 0·967. The total values were: for *s* 0·974 — highly significant; for *n* 0·849—not significant; for $G \simeq 1{\cdot}00$ — highly significant.

Although cycles of 10·5 months gave the best fit to the present *s* values, subsequent sampling since September 1976 indicate that maxima occur annually in September and a 12-monthly period has been used to calculate the constants in the generalized equation,

$$s = \tfrac{1}{2}A^\circ + A\cos\left(\frac{2\pi t}{T}\right) + B\sin\left(\frac{2\pi t}{T}\right)$$

where $\tfrac{1}{2}A^\circ = 3{\cdot}20$

$A = 19{\cdot}28$

$B = -17{\cdot}27$

$T = 12{\cdot}0$

Combining the linear and cyclic components gives,

$$s = 19{\cdot}28\cos\left(\frac{2\pi t}{12}\right) - 17{\cdot}27\sin\left(\frac{2\pi t}{12}\right) + 5{\cdot}25\ t + 32{\cdot}0$$

This curve, superimposed on the data in Fig. 8a shows good agreement, and while reducing the R^2 value from 0·974 to 0·968, it still remains highly significant to the 0·01 level.

DISCUSSION

FAUNISTIC COMPOSITION

The total number of species (263) is less than the total species reported from Moreton Bay (Southern Region — 394 by Stephenson et al. 1974; central region — 182 by Raphael 1974; Middle Banks — 463 by Stephenson et al. 1978) and similar to the number from Port Curtis (251 — Stephenson et al. 1979), but greatly exceeds the number of species so far recorded from southeastern Queensland estuaries (98 — Serpentine Creek, Stephenson and Campbell 1977; 64 — eight estuaries sampled once after the 1974 floods, Campbell et al. 1974).

In other Australian estuarine studies, the following numbers of macrobenthic species have been recorded: 55 — Blackwood River Estuary, W.A. (Hodgkin 1978); 74 — Wallis Lake, N.S.W. (Hutchings et al. 1978); 158 — Careel Bay, N.S.W. (Hutchings and Recher 1974); 246

— Port Phillip Bay, V. (Poore and Kudenov 1978) and 571 — Westernport Bay, V. (Coleman et al. 1978).

In terms of the numbers of organisms per square metre, the benthos of the Calliope River and Auckland Creek is compared with other southeastern Queensland estuaries (Table 11). The large numbers of *Apseudes estuarius* as found in Ninghi, Cabbage Tree and Serpentine Creeks (Campbell et al. 1974; Stephenson and Campbell 1977) have not been observed. Classification of species-groups in site-groups indicated that an 'upstream' community exists in the Calliope River, of which *A. estuarius* is a predominant component; it is thus possible that sampling further upstream than at present may have resulted in higher numbers of individuals per square metre.

Site/Species Classification

The classification of sites using their biotic composition gave site-groups which were easily characterized abiotically (Table 7), and it indicates that sites can be grouped according to their upstream/downstream position, the sediment type and the depth below low water. Classification of species using their standardized occurrences within site-groups, enabled site-groups to be characterized by the presence or absence of certain species-groups (Table 10).

TABLE 11: Numbers of Benthic Organisms per M^2 Recorded from Queensland Estuaries.

System	n/m^2
Calliope River*	0 – 3,540
Auckland Creek*	0 – 1,950
Noosa River	80 – 6,080
Maroochy River	40 – 6,240
Mooloolah River**	463 – 6,481
Ninghi Creek	100 – 15,840
Caboolture River	200 – 11,680
Pine River	340 – 8,660
Cabbage Tree Creek	520 – 33,140
Serpentine Creek***	132 – 14,128
Logan River	20 – 3,060
Coomera River	140 – 1,360
Nerang River	0 – 360

* Present survey
** Saenger unpubl. data
*** Stephenson and Campbell, 1977
Other data based on Campbell et al, 1974

A point that merits emphasis is that with the exception of the upstream areas, the shallow-water and deeper-water biotas at a given distance upstream were quite different; a similar pattern was observed in Serpentine Creek (Stephenson and Campbell 1977). One obvious implication of this finding in relation to baseline benthic surveys is that to adequately sample an area, across-river transects should be used.

Times Classification/Periodicities

Times classification showed high times dissimilarities; initially this suggested that sampling times were too infrequent; however two times showed low values of s and n (T_2 and T_5), both were in late summer and both lacked two times-based species-groups; this suggests a seasonal component. Cyclic analyses of summated parameters confirmed this but indicated that an underlying non-cyclic trend was also present. The underlying linear trend was zeroed at −8·8 months i.e. January 1974, using the average estimate from s and G.

December 1973 and January 1974 were particularly wet months with unusually heavy rainfall and river flow rates (Table 12), and extensive flooding occurred during this period. In fact on the 20 December 1973, a flow rate of 172,000 megalitres was recorded for the preceding 24-hour period; this 24-hour flow rate is comparable to the mean annual flow rate of normal years (Table 1). In view of this flooding, it became apparent that the benthic data could be best interpreted as a recolonization situation following a 'catastrophic' disturbance, and a model is proposed.

TABLE 12: Gladstone Rainfall and Calliope River Discharges During October 1973 to May 1974.

Month	Monthly Rainfall (mm)*	Monthly River Discharge (megalitres)**
October	43	2,065
November	127	4,751
December	433	401,863
January	640	254,718
February	43	31,652
March	38	8,590
April	29	5,051
May	27	3,514

* Supplied by Department of Meteorology
** Supplied by Water Resources Council of Queensland, from Castlehope Measuring Station.

RECOLONIZATION MODEL

It is postulated that the intense flooding of December–January 1974 led to a more or less complete removal of the benthic fauna as a result of the combination of reduced salinity, physical scouring of the estuary and reduced oxygen levels. These factors have been identified as reducing the benthos elsewhere (Stephenson et al. 1977; Stephenson et al. 1979; Rosenberg 1977; Boesch et al. 1976).

On returning to normal conditions, recolonization would commence. Evidence of recolonization comes from a superficial survey carried out in November 1973 (before flooding) near the power station site, which revealed 44 benthic species (A. Maluish unpubl. data). Another survey, during which 3 sites were sampled near the power station in April 1974 (after flooding), revealed 'no organisms where these would have been expected' (B. Campbell pers. comm.).

The present data suggest that the re-appearance of species is more or less linear over a period of 29 months (Fig. 8a) while the numbers of individuals of all species increase logarithmically (Fig. 8c) during this period. Wolff et al. (1977) followed the colonization of a newly-formed seawater lake for 4·5 years and found that the numbers of individuals increased logarithmically over the entire 4·5 years. A linear increase in the number of species was found over the initial 27 months, but after this time, the number of species did not increase further.

It could be expected that after a massive disturbance, opportunistis benthic species would be the initial recolonizers (Grassle and Grassle 1974; Boesch et al. 1976; Rhoads et al. 1978) with other species reappearing later. The cumulative number of species recorded at various times (Fig. 9) during the study indicates that new species arrived throughout the study, even though the cumulative number at each transect approaches a maximum (Fig. 9). This in turn suggests that genuine changes (as distinct from sampling inadequacies) in the species composition occurred during the 20 months of the study.

In terms of the time scale involved, recolonization after 'catastrophic' and 'seasonal' events must be distinguished. Recovery after seasonal disturbance (e.g. freshwater inflow, high temperatures etc.) seems to occur in approximately 3 months in the present study area (Fig. 8a). In Port Curtis, seasonal recovery occurred after 2–3 months (Stephenson et al. 1979); in a west African estuary a period of 1–2 months was observed (Sandison and Hill 1959) while in a Dutch estuary, seasonal recovery occurred at 2–3 months (Wolff et al. 1977).

Recovery from non-seasonal 'catastrophic' events takes longer and depends on the severity of the disturbance: MacGinitie (1939) reports recolonization after flooding was completed in 9 months; Kaplan et al. (1975) found that the benthos of a dredged channel had not recovered after 11 months; Stephenson et al. (1977) found general recovery 13 months after flooding in Bramble Bay, Queensland; Rhoads et al. (1978) found that colonization of spoil dumps required 1·5–2 years; Watson (1973) estimated that recovery of the benthos after pipeline dredging in Port Phillip Bay, Victoria, would be complete within 2 years; Boesch et al. (1976) found that the benthos had not recovered from the effects of a tropical cyclone after 2·5 years; Wolff et al. (1977) found that species numbers approached a maximum in a new seawater lake after 2·5 years. In the present study, the number of species has not approached a maximum within 29 months after severe flooding (Fig. 8a and 9), although preliminary analyses of subsequent survey data (T_8 — November 1976 to T_{18} — July 1979) suggest that recovery was more or less complete after 5 years.

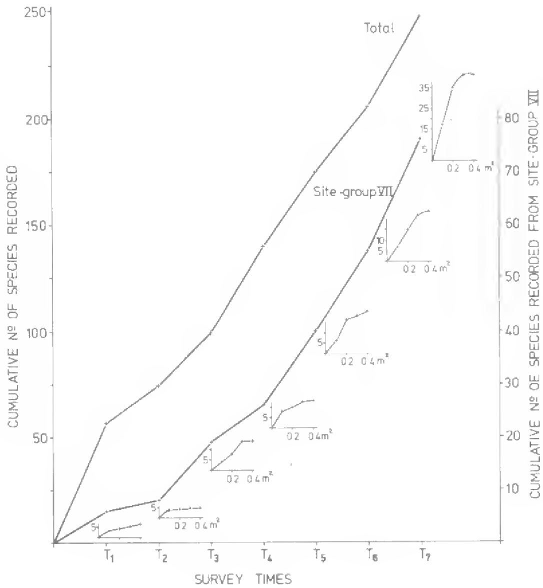

FIG 9: Cumulative number of species recorded for all site-groups and for site-groups VII. Species-area curves for catches at site-group VII are also shown.

While the present model, like all models, has tentative aspects, the data summarized in Figs. 8 and 9 show that the 'pre-thermal' situation is not a stable one, and that progressive changes are occurring. Since these can be expected to continue to occur, two elements are likely to interact during the 'post-thermal' times i.e. recovery from flooding and thermal effects. It will be essential to allow for the former in assessing the latter.

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APPENDIX
RIVER BENTHOS SPECIES LIST WITH CODE NUMBERS

(* indicates new species or major extension of range)

ALGAE
1 *Champia parvula*
2 *Enteromorpha clathrata*
3 *Heterosiphonia multiceps*
4 *Laurencia obtusa*
5 *Lophocladia* sp.
6 *Polysiphonia flaccidissima*
7 *Crouania* sp. nov.*
8 *Sporochnus comosus*
9 *Spyridia filamentosa*
10 *Ulothrix* sp.
11 *Callithamnion* sp.
12 *Soliera robusta*
13 *Griffithsia* sp.
14 *Ceramium cliftonianum*

SEAGRASSES
26 *Halophila decipiens*

COELENTERATA
31 ANTHOZOA sp. I
32 ANTHOZOA sp. II
33 *Virgularia gustaviana*
34 *Dendronephtya (Morchellana)* sp.*
35 *Virgularia gracillima*

NEMERTEA
46 Unident sp. I

ECHIURA
51 ECHIURIDAE sp. I

PLATYHELMINTHES
56 Stylochid sp. A
57 Planocerid sp. A

BRYOZOA
61 *Bugula* cf. *uniserialis*

POLYCHAETA
66 *Amaeana trilobata*
67 *Ampharete* sp.
68 *Armandia intermedia*
69 *Branchiomma* sp.
70 *Cirratulus* sp.
71 *Cirriformia* sp.
72 *Capitella* sp.
73 *Coppingeria longisetosa*
74 *Ceratocephala* sp.
75 *Diopatra* sp.
76 *Glycera americana*
77 *Glycera* sp.
78 HESIONIDAE sp. I
79 *Heteromastus* sp.
80 HETERONEREIIDAE sp. I
81 *Harmothoe* sp.
82 *Lysilla apheles*
83 *Lysilla pacifica*
84 *Laonice* sp.
85 *Leitoscoloplos normalis*
86 *Leitoscoloplos* sp. nov.*
87 *Lumbrinereis* sp.
88 *Lepidonotus* sp.
89 MAGELONIDAE sp. I
90 MALDANIDAE sp. I
91 *Mediomastus* sp.
92 *Marphysa sanguinea*
93 *Maldane* sp.
94 NEREIIDAE sp. I
95 *Nephtys mesobranchia**
96 *Notomastus* sp.
97 OPHELIIDAE sp. I
98 *Ophelina* sp.
99 *Owenia fusiformis*
100 *Poecilochaetus serpens*
101 *Poecilochaetus* sp.
102 *Pista pectinata*

103 *Pista* sp. nov.*
104 *Prionospio queenslandica*
105 *Polydora* sp.
106 POLYONIDAE sp. I
107 *Phyllodoce* sp. I
108 *Phyllodoce* sp. II
109 *Pectinaria* sp.
110 *Scyphoproctus* sp.
111 *Scoloplos implex*
112 *Scoloplos johnstonei*
113 *Sthenolepis* sp.
114 *Sternaspis scutata*
115 *Stenelais* sp.
116 *Streblosoma amboinense*
117 *Streblosoma* sp.
118 TEREBELLIDAE (s.f. Thelepinae) sp. I
119 *Terebellides stroemi*
120 *Thelepus setosus*
121 *Pseudopolydora kempi*
122 *Onuphis* sp.
123 *Isolda pulchella*
124 *Magelona dakini*
125 *Laonome* sp.
126 *Australonereis ehlersi*
127 SERPULID sp. I
128 *Ancistrosyllis* sp.
129 OLIGOCHAETE sp. I
130 *Cossura* sp.
131 *Aonides* sp.
132 *Eunice* c.f. *australis*
133 *Ceratonereis erythraeensis*
134 *Euclymene* sp.
135 *Mediomastus californiensis*
136 *Scolelepis* sp.
137 *Syllis* sp. I
138 CHAETOPTERIDAE sp. I
139 SABELLIDAE sp.
140 *Spio pacifica*
141 *Ophiodromus* sp.
142 *Syllis* sp. II
150 *Phoronis* sp.

NATANTIA
151 *Alpheus* sp.
152 *Metapenaeopsis* sp.
153 *Parapenaeopsis* sp.
154 *Metapenaeus bennettae*
156 *Lysmata* sp.
157 *Macrobrachium intermedium*
158 *Latreutes mucronatus*
159 *Ogyrides delli*
160 HIPPOLYTIDAE sp. II
162 *Lucifer* sp.

BRACHYURA
176 *Acheus lacertosus*
177 *Australoplax tridentata*
178 *Dorippa astuta*
179 *Dorippa* sp.
180 *Elamenopsis lineata*
181 *Eucrate* sp.
182 *Halicarcinus australis*
183 *Halicarcinus* sp. A
184 *Halicarcinus bedfordi*
185 *Heteropanope* sp.
186 *Hyastenus* sp.
187 *Ilyoplax dentatus*
188 *Ilyoplax orientalis*
189 *Macrophthalmus punctulatus*
190 *Macrophthalmus latreillei*
191 *Matuta* sp.
192 *Neorhynchoplax* sp.
193 *Nursia abbreviata*
194 *Paracleistostoma mcneilli*
195 *Petrolisthes teres*
196 *Petrolisthes* cf. *scabriculus*
197 *Petrolisthes* sp. nov.
198 *Phalangipus* sp.
199 *Pilumnus* sp. A
200 *Pilumnus* sp. B
201 *Pilumnus* cf. *hirsutus*
202 *Portunus pelagicus*
203 *Raphidopus cilatus*
204 *Sesarma semperi longicristatum*
205 *Uca* sp.
206 *Xenophthalmus pinnotheroides*

AMPHIPODA
226 AMPELISCIDAE sp.
227 AMPHIPODA sp. I
228 AMPHIPODA sp. II
229 AMPHIPODA sp. III
230 AMPHIPODA sp. IV
231 AMPHIPODA sp. V
232 AMPHIPODA sp. VI
233 AMPHIPODA sp. VII
234 CAPRELLIDAE sp. I
235 CAPRELLIDAE sp. II
236 *Ceradocus* sp.
237 *Corophium* sp.
238 *Dryopoides* sp.
239 *Ericthonius* sp.
240 *Eriopisa* sp. I
241 *Eriopisa* sp. II
242 *Grandidierella* sp. I
243 *Grandidierella* sp. II
244 *Grandidierella* sp. III
245 *Maera* sp. I
246 *Maera* sp. II
247 *Melita* sp.
248 *Oedicerateda* sp. I
249 *Oedicerateda* sp. II
250 *Paracorophium* sp.
251 *Paraphoxus* sp.
252 *Quadrivisio* sp.
253 AMPHIPODA VIII

OTHER CRUSTACEANS
276 *Apseudes estuarius*
277 *Apseudes* sp. II
278 *Apseudes* sp. III
279 *Tanais* sp.
281 OSTRACODA sp. I
282 OSTRACODA sp. II
285 *Pomacuma australiae*
286 *Dimorphostylis australis*
287 *Eocuma agrion*
288 *Cyclaspis ? usitata*
289 *Campylaspis latidactyla*
294 PAGURIDAE sp. I
295 MYSIDAE sp. I
296 MYSIDAE sp. II
297 MYSIDAE sp. III
298 MYSIDAE sp. IV

ISOPODA
301 *Mesanthura* sp.
302 *Sphaeroma* sp.
303 *Synidotea* sp.
304 *Paracereis* sp.
305 *Eurydice sp.*

STOMATOPODA
311 *Squilla* sp.
312 *Callianassa* sp.
313 *Thalassina anomala*

PYCNOGONIDAE
316 *Propallene saengeri**
317 *Hemichela* sp. nov.*
318 *Anoplodactylus tubiferus**

GASTROPODA
326 *Aglaja* sp. nov.*
327 *Atys* sp.
328 *Bedeva hanleyi*
329 *Cerithideopsilla cingulata*
330 *Haminoea* sp.
331 *Nassarius burchardi*
332 *Nassarius dorsatus*
333 *Nassarius* sp.
334 *Polynices sordida*
335 *Pseudoraphitoma* sp.
336 *Ringicula* sp.
337 *Zafra* sp.
338 *Zeacumantus* sp.
339 *Philine* sp. nov.
340 *Tornatina* sp.
341 *Trinchesia* sp.
342 *Facelinella* sp.

PELECYPODA
351 *Anomia descripta*
352 *Amygdalum* sp.
353 ARCIDAE sp. I
354 *Barnea* sp. I
355 *Barnea* sp. II
356 *Circe* cf. *australis*
357 *Circe* sp. II
358 *Corbula* sp.
359 *Didimacar repeata*
360 *Ennucula* sp.
361 *Ensiculus cultellus*
362 *Fluviolanatus amarus*
363 *Gari lessoni*
364 *Gouldia* sp. I
365 *Gouldia* sp. II
366 *Laternula* sp. I
367 *Laternula* sp. II*
368 cf. *Laternula* sp.
369 *Limaria noverea*
370 *Mactra* sp.
371 *Modiolus auriculatus*
372 *Notospisula parva producta*
373 *Nuculana* sp.
374 *Pharella wardi*
375 *Placamen* sp.
376 *Saccostrea* cf. *cucullata*
377 *Solecurtus* sp.
378 *Solen correctus*
379 *Tapes hiantina*
380 *Tellina semen*
381 *Tellina* sp.
382 *Trisidos tortuosa*
383 VENERIDAE sp. I
384 *Volachlamys singaporinus*
400 *Dentalium* sp.

ECHINODERMATA
401 *Amphioplus personatus*
402 *Amphioplus hastatus*
403 *Amphiura bidentata**
404 *Amphiura leptotata**
405 *Amphiura micra**
406 *Amphiura phrixa**
407 *Amphiura tenuis**
408 *Protankyra verrilli*
409 *Amphiura octacantha**
410 *Amphipholis squamata*

TUNICATA
426 *Ascidia sydneyensis*
427 *Molgula mollis*
428 *Cnemidocarpa etheridgii*
429 *Microcosmus australis*

PISCES
451 APOGONIDAE sp. I
452 *Brachyamblyopus* cf. *urolepis*
453 *Drombus palackyi*
454 *Prionobutis microps*
455 *Favonigobius* sp.

Mem. Qd Mus. **20**(1): 163–70, [1980]

THE ISOPOD GENUS *DYNAMENE* FROM AUSTRALIAN WATERS, WITH DESCRIPTION OF A NEW SPECIES FROM CORAL REEFS

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ABSTRACT

A new species of the isopod genus *Dynamene*, *D. curalii*, is described from the coral habitat of Heron Island and Lizard Island in Queensland. The only other species of this genus known from the Southern Hemisphere, *D. ramuscula* Baker from South Australia, is redescribed. It is noted that the two Australian species differ markedly in one of the diagnostic characters when compared with species from Europe and N.W. Africa.

Seven species of the sphaeromatid isopod *Dynamene* Leach, 1814 are known to date (Holdich 1968a, 1970). Of these species *D. bidentata* (Adams) is known only from the Atlantic coasts and islands of N.W. Africa and Western Europe; *D. magnitorata* Holdich from the coasts of continental Western Europe (Holdich 1976), the Azores, and Mediterranean; *D. edwardsi* Lucas has been recorded from Atlantic coasts of Europe and N.W. Africa but mainly occurs in the Mediterranean, Aegean and Red Sea; *D. bifida* Torelli and *D. tubicauda* Holdich appear to be restricted to the Mediterranean; and *D. torelliae* Holdich occurs in the Mediterranean, Adriatic, Aegean, and also extends into the Black Sea. These species therefore appear to be restricted in their distribution to Western Europe, N.W. Africa and the Mediterranean and adjacent seas. There have been frequent misidentifications in the past (Holdich 1968a for review) but the only valid record for a species outside that area is *D. ramuscula* Baker from South Australia. This species appears, from the literature, to closely resemble *D. bifida*.

The only low latitude record for a *Dynamene* species is for *D. edwardsi* from southern Spanish Sahara (latitude 22°N). In this paper a new species is described from coral reefs in Queensland, Australia which appears to have a tropical and sub-tropical distribution. When comparing the new species with the type specimens of *D. ramuscula* it was discovered that the latter species in fact differs notably from *D. bifida* and a redescription was considered necessary.

SYSTEMATICS

Order ISOPODA
Family SPHAEROMATIDAE
Sub-family EUBRANCHIATINAE

Dynamene Leach, 1814

Generic Diagnosis

Eubranchiate sphaeromatid with body approximately elliptical. Anteriorly, cephalosome separating the bases of the antennules. Eyes set slightly into pereonal tergite 1. Coxal plates of pereonites 1–7 separated from tergites by sutures. Pereonal tergite 7 reduced, not reaching lateral margins of body. Each side of the pleonal tergite bearing two short, postero-lateral incisions. Pleotelson domed, bearing an obvious terminal notch which may be enclosed forming a tube. Antennular peduncle articles 1 and 2 dilated and juxtaposed to ventral margin of cephalosome. All pereopods ambulatory. Both rami of pleopods 1–3 bearing margin of plumose seate. Endopods of uropods juxtaposed to pleotelsonic margin; exopods posteriorly directed. Sexual dimorphism pronounced. Adult male with pereonal tergite 6 longer than those preceding, posterior margin with an elongate, posteriorly

directed process either side of mid-line. Pleotelson bearing transverse, bilaterally symmetrical ornamentation. Penes small, separate. Endopod of pleopod 2 lacking appendix masculina. Ovigerous female with pereonal tergite 6 similar to those preceding. Pleotelson smooth. Young incubated in a marsupium, formed from four pairs of lamellae which arise from pereonites 1–4. Mouthparts strongly metamorphosed.

Dynamene curalii sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W6319, male, from *Lithothamnion* sp. behind reef crest, intertidal, Heron Island, SEQ, D.M. Holdich, 15 April 1976.

ALLOTYPE: QM W6320, ovigerous female, same data as Holotype.

PARATYPES: QM W6321, juvenile, from *Halimeda* sp. behind reef crest, intertidal, Heron Island, SEQ, D.M. Holdich, 15 April 1976. QM W6322, sub-adult male, behind reef crest opposite research station, intertidal, Heron Is., SEQ, N. Bruce, 6 June 1978. QM W6323, non-ovigerous female, same data as W6322.

OTHER MATERIAL

Heron Island, Queensland, from *Lithothamnion* sp. behind reef crest, Intertidal, 4 adult males, 2 ovigerous females, 1 juvenile, Coll. D.M. Holdich, 15 April 1976. North Point, Lizard Island, Queensland, On *Halimeda* sp. associated with coral at 9·0 m, 1 sub-adult male, Coll. B. Barnett, 8 June 1976. Heron Island, Queensland, Behind reef crest opposite research station, Intertidal, 2 adult males, 1 sub-adult male, 4 ovigerous females, 2 juveniles, Coll. N. Bruce, 6 June 1978.

DESCRIPTION

ADULT MALE: (Figs. 1a – c, f – h; 2d – v). Body deeply vaulted, not depressed. Dorsal surface and lateral margins bearing long setae. Frontal region of cephalosome, between antennules, sub-equal in width to labrum. Pereonal tergite 1 sub-equal in length to cephalosome and twice as long as tergite 2. Tergites 2–5 sub-equal. All coxal plates directed ventrally, not expanded. Pereonal tergite 6 three times as long as tergite 5 and rugose in its posterior half. Posterior projections rugose, simple (i.e. not bifid), widely separate, just more than half length of tergite. Posterior tergal margin, lateral to the projections, straight, bearing no secondary projections. Postero-lateral margin of pereonal tergite 7 as a simple lobe, not bifid. Pleonal tergite rugose laterally. Pleotelson bearing a short, simple or multispined tubercle either side of the mid-line. Pleotelsonic foramen with sub-triangular, serrate lip; entirely enclosed ventrally, forming a tube.

Antennule with peduncle articles 1 and 2 setose; 1 slightly longer than 2, bearing a distal inferior spine; 2 bearing a proximal, inferior, curved spine and a distal infero-dorsal spine. Distal region of article 2 acute. Antennular flagellum of six articles, 2–5 each bearing one long aesthetasc. Antennal peduncle not expanded; flagellum of seven articles, last very reduced.

Mouthparts: labrum slightly wider than long with setose distal margin; proximal region set into the broad epistome which has a straight anterior margin. Mandibles with incisor processes, molar processes and palps well developed. Maxillule with tip of inner lobe bearing four pectinate setae and outer lobe bearing approximately ten stout, curved spines. Maxilla with two outer lobes bearing long, curved, robust, simple setae, and inner lobe bearing eight long, robust, pectinate setae. Maxillipedal endite four times as long as broad with stout, plumose, apical setae. Inner margin bearing one coupling hook. Palp of five articles; 1 reduced, 2–4 bearing pronounced, narrow lobes, 2–5 with apical, plumose setae. Pereopods all ambulatory, first slightly more robust than remainder. Dactylus of each with pronounced secondary unguis. Merus, carpus and propus bearing stout setae on superior and inferior surfaces. Penes small, separate.

Pleopods: pleopod 1 with internal margin of basis extended medially beyond rami, bearing three coupling hooks. Rami sub-elliptical, each bearing apical, plumose setae equal in length to ramus, lateral simple setae and several long, non-marginal setae. Endopod two-thirds length of exopod. Basis of pleopod 2 bearing three coupling hooks. Endopod sub-triangular; exopod ovate with several proximal, non-marginal setae. Both rami bearing long, plumose, terminal setae. Basis of pleopod 3 rectangular with three coupling hooks. Endopod sub-triangular, twice as long as elliptical exopod. Both rami with terminal, and exopod also with external, plumose setae, those on exopod twice as long as those on endopod. Both rami of pleopod 4 sub-ovate, bearing respiratory folds along entire length. Apex of exopod thickened, toothed; external margin with proximal, toothed process. Apex of endopod acute, curved medially. Both rami of pleopod 5 extensively pleated. Endopod sub-elliptical with apex broadly rounded, bearing fine setae. Exopod sub-ovate with three very pronounced, toothed apical processes. Both rami of all pleopods lacking articulations. Uropods

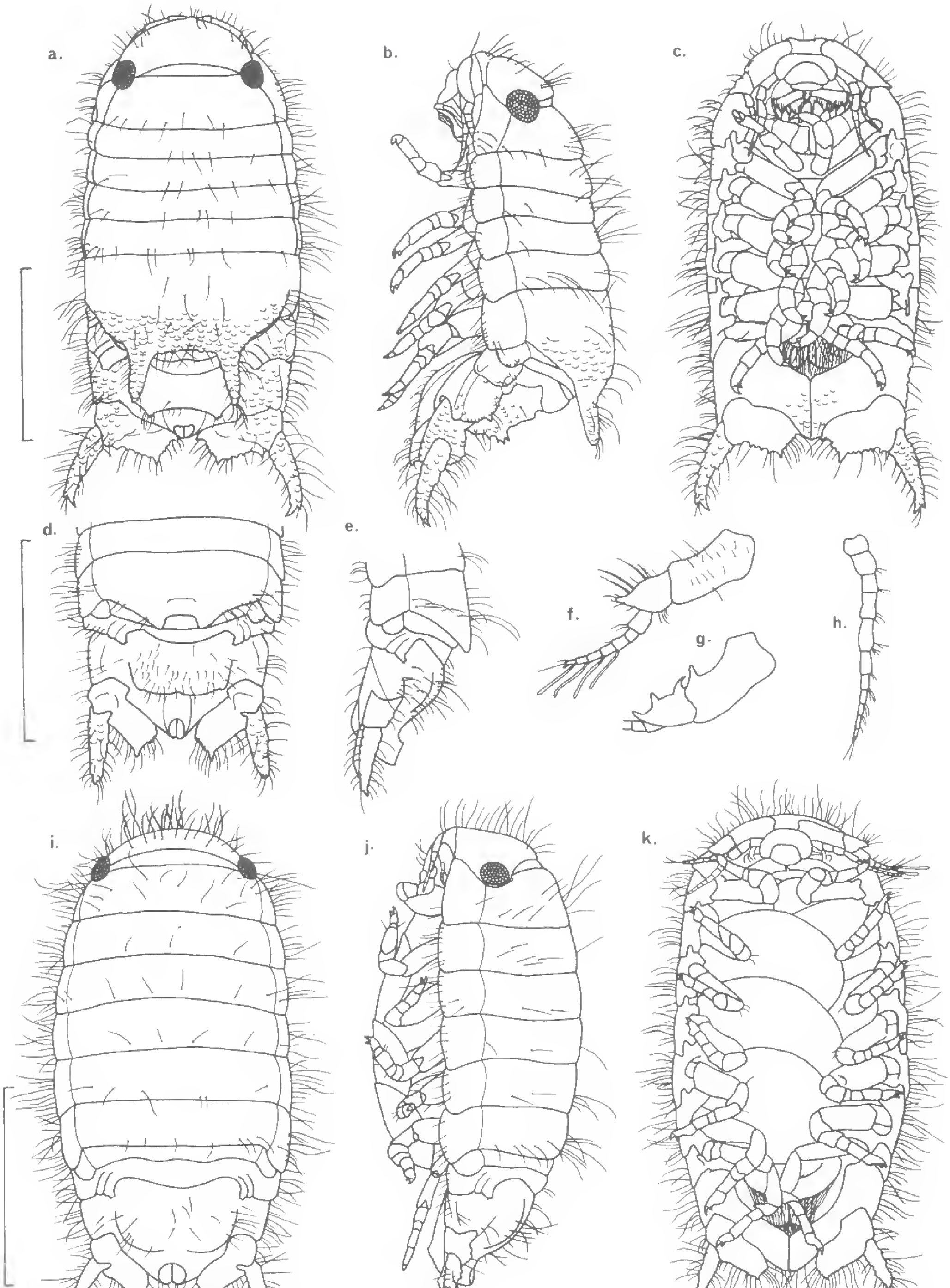

FIG. 1: *Dynamene curalii* sp. nov. Adult male (a) dorsal, (b) lateral, (c) ventral, (f) right antennule, ventral view, (g) right antennular peduncle, antero-dorsal view, (h) left antenna. Sub-adult male posterior region (d) dorsal, (e) lateral. Ovigerous female (i) dorsal, (j) lateral, (k) ventral. Scales represent 1 mm.

with wide, rectangular endopods, each internal corner bearing a pronounced spine. Margins straight or markedly spined, setose. Exopod setose, rugose, sub-cylindrical, tapering to an acute, medio-dorsally directed apex bearing a short, external, accessory spine.

Body length: 2·44 mm.

SUB-ADULT MALE: (Fig. 1d, e). Pereonal tergite 6 twice as long as 5, posterior margin bearing a short, blunt projection either side of the mid-line. Projections on pereonal tergite not contiguous. Pleotelson domed, setose, lacking obvious rugosity and ornamentation. Pleotelsonic foramen sub-circular, smooth-lipped. Penes present as minute separate papillae. Uropod with rectangular endopod bearing a spine on the medio-posterior corner. Exopod sub-cylindrical, rugose, sub-equal in length to endopod, with a curved, acute tip.

Body length: 2·12 mm.

OVIGEROUS FEMALE: (Figs. 1i–k; 2w–z). Pleotelsonic foramen sub-circular, directed dorsally, completely enclosed ventrally forming a tube. Pereopods as in male, no obvious increase in setation. Four pairs of brood lamellae well developed, overlapping considerably in mid-line. Approximately twelve eggs in brood pouch. Uropod with rectangular endopod, either lacking spines or with a single medio-posterior spine. Exopod rugose, sub-cylindrical, sub-equal in length to endopod, lacking curved, acute tip.

Body length: 2·3 mm.

NON-OVIGEROUS FEMALE: (Fig. 2a, b). Pleotelson more domed than in ovigerous female, with foramen sub-circular, smooth-lipped, directed postero-dorsally. Antennule bearing two aesthetascs. Exopod of uropod with acute terminal spine.

Body length: 2·48 mm. There is a tendency for some *Dynamene* species to decrease slightly in apparent length at the ovigerous moult (Holdich 1968b) hence the difference in the lengths of the non-ovigerous and ovigerous females recorded here.

JUVENILE: (Fig. 2c). Body slightly depressed, coxal plates directed laterally. Pleotelsonic foramen sub-circular, directed posteriorly. Exopod of uropod acute, sub-equal to endopod.

REMARKS

Dynamene curalii can be separated from all known species of *Dynamene*, except *D. tubicauda*, by the lack of a central pleotelsonic boss in the adult male. Unlike *D. tubicauda*, however, the adult male of *D. curalii* is not depressed, the anterior region of the cephalosome is not extended as a shelf and the exopods of the uropods bear incurved, acute apices. (See also remarks following *D. ramuscula*).

ETYMOLOGY: *Dynamene* + L. *curalii* i.e. of coral.

ECOLOGY AND LIFE-CYCLE

On Heron Island this species occurs intertidally on and behind the reef crest. As with other *Dynamene* species (Holdich 1968b, 1970, 1976) the adults take up a crytozoic existence for the terminal reproductive phase of their life-cycle, occupying small cavities amongst dead coral and lithified algae. In some cases the habitats are exposed to strong wave action.

As the ovigerous females undergo marked degeneration at the ovigerous moult (as in other species of *Dynamene*) they probably die after release of the brood. Juveniles, after release from the brood pouch, settle and feed on various species of algae on the reef. It is not known how long the growth phase of the life-cycle is, or whether males spend one or two breeding seasons in the reproductive habitat.

On Lizard Island two sub-adult males were collected (one subsequently escaped) from sub-littoral algae thus indicating that *D. curalii* is not restricted to the intertidal zone.

Other species of isopod which have a biphasic life-cycle occur in similar reproductive habitats to *Dynamene* and probably compete with it for space. Notable amongst these is the genus *Gnathia* Leach which has recently been found to be a common element in cryptic habitats in Queensland (Holdich and Harrison, 1980).

Dynamene ramuscula Baker, 1908

Dynamene ramuscula Baker, 1908, pp. 45–6, 161, pl. 5; Hale, 1929, pp. 293–4; Monod, 1932, p. 64; Holdich, 1968a, pp. 412–3; 1970, p. 422.

Dynamene ramusculus Nierstrasz, 1931, p. 211. (Unjustified emendation).

MATERIAL EXAMINED

South Australian Museum reg. no. C.355. 2 males, 2 ovigerous females, St. Vincent Gulf, South Australia. On sponges.

DESCRIPTION

ADULT MALE (Fig. 3a–k, n–p). Body deeply vaulted, not depressed. Dorsal surface, uropods

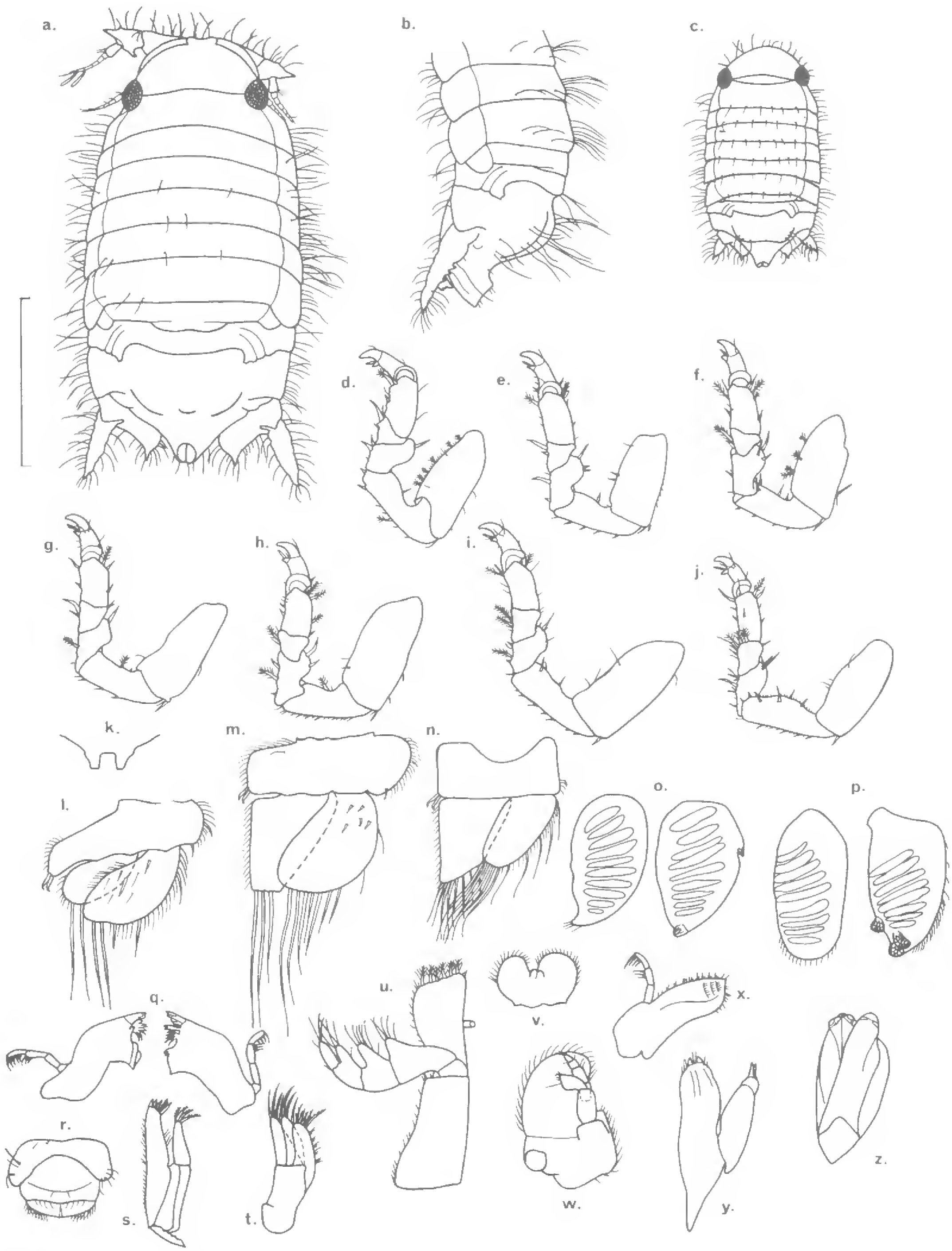

FIG. 2: *Dynamene curalii* sp. nov. Non-ovigerous female (a) dorsal, (b) lateral, posterior region. Juvenile (c) dorsal. Adult male (d–j) pereopods 1–7 respectively, (k) penes, (l–n) pleopods 1–3 respectively, (o) rami of pleopod 4, (p) rami of pleopod 5, (q) mandibles, posterior view, (r) labrum and epistome, (s) maxillule, (t) maxilla, (u) maxillipede, (v) paragnaths. Ovigerous female (w) maxillipede, (x) mandible, (y) maxillule, (z) maxilla. Scale represents 1 mm.

and ventral surface of pleotelson bearing long setae. Frontal region of cephalosome, between antennules, narrow, one quarter width of labrum. Pereonal tergite 1 sub-equal in length to cephalosome and twice as long as tergite 2. Tergites 2–5 sub-equal, each rugose in posterior half. All coxal plates directed ventrally, not expanded. Pereonal tergite 6 more than twice as long as tergite 5, rugose. Posterior projections sinuous, contiguous in mid-line, diverging distally, sub-parallel terminally, each bearing a ventrally directed, sub-terminal, accessory projection. Posterior tergal margin bearing a slight, rugose tubercle mid-way between projection and coxal plate on each side. Postero-lateral margin of pereonal tergite 7 as a simple lobe, not bifid. Pleonal tergite rugose, obscure in dorsal view. Pleotelson rugose, having a quincunx of acute, conical tubercles, the central being the largest, with a smaller, conical tubercle anterior to the basis of each uropod. Pleotelsonic foramen sub-triangular, closed ventrally forming a tube.

Antennular peduncle with article 1 having a short, blunt, distal, inferior spine; 2 with a larger, wide, proximal, inferior spine and a blunt apex. Flagellum of eight articles, 3–8 each bearing a single aesthetasc. Antennal peduncle not expanded, flagellum of nine articles, distal article reduced.

Mouthparts: labrum sub-circular, semi-enclosed by V-shaped epistome. Mandible with well formed incisor process, molar process and palp, Palp article 2 with five distal, inferior setae. Left mandible with tridentate incisor process, tridentate lacinia mobilis and setal row of six pectinate setae. Maxillule and maxilla of usual sphaeromatid form. Maxillipedal endite four times as long as broad. Palp articles 2–4 with pronounced superior lobes, relatively longer than those of *D. curalii* sp. nov. Pereopods all ambulatory, first slightly more robust than remainder, with reduced carpus and inferior margins of merus, carpus and propus bearing long, stout, simple spines. All pereopods with pronounced secondary unguis, 2–7 with variable setation on inferior margins. Penes short, widely separate at base.

Pleopods: pleopod 1 with internal margin of basis not extending medially beyond rami. Rami sub-elliptical with long, terminal and external, marginal, plumose setae. Endopod three quarters length of exopod. Pleopod 2 with endopod sub-triangular, exopod sub-ovate. Rami sub-equal in length, each bearing long, terminal and external setae. Pleopod 3 with endopod twice length of exopod. Endopod sub-triangular with short, terminal, plumose setae. Exopod sub-ovate with terminal, plumose setae extending beyond tip of endopod. Pleopod 4 of specimen damaged, but external margin of exopod having proximal, toothed process. Both rami of pleopod 5 with respiratory folds. Endopod sub-elliptical with apical border of short, fine setae. Exopod sub-elliptical with truncate base. Apex as a short, wide, toothed region with a prominent sub-terminal toothed process and a toothed region on the distal, internal margin. All observed pleopodal rami lacking articulations. Uropods with basis bearing conical, dorsal tubercle. Endopod rugose, with a blunt, distal, posterior spine; antero-medial margin smoothly rounded; posterior margin uneven. Exopod one and a half times length of endopod, sub-cylindrical, rugose, acute tip lacking accessory spine.

Body length: 4·23 mm.

Ovigerous Female (Fig. 3 l, m)

Body sub-elliptical, setose; lateral pereonal margins strongly convex. Pleotelson with low, median tubercle. Sub-circular foramen directed postero-dorsally, enclosed ventrally forming a tube. Uropod with rami sub-equal, smoothly rounded apically.

Body length: 4·23 mm.

Remarks

The similarity between *D. ramuscula,* as figured by Baker (1908) and *D. bifida* from the Mediterranean has been mentioned in the literature (Monod 1932, Holdich 1968a). In fact these two species can be easily separated by the very different nature of the pleotelsonic ornamentation of the males (that of *D. bifida* being restricted to a single, central, low, bifid boss) and by the form of the posterior pereonal projections in the male (those of *D. bifida* being sub-parallel, separate at the base and not markedly divergent).

Etymology: *Dynamene* + L. *ramuscula* i.e. branching, like a twig.

Discussion

The occurrence in Australia of a second species of *Dynamene* is very noteworthy. Previously, only *D. ramuscula* from South Australia was known. This species has only been recorded once. Examination of specimens of *D. bifida* and *D. ramuscula* have shown conclusively that, on morphological grounds, they are distinct species.

FIG. 3: *Dynamene ramuscula* Baker. Adult male (a) dorsal, (b) lateral, (c) ventral, (d) pereopod 1, (e) pereopod 3, (f) maxillipede, (h) antennule, (i) antenna, (g, j, k) pleopods 1–3 respectively, (n) proximal external margin of damaged exopod of pleopod 4, (o) exopod of pleopod 5, (p) endopod of pleopod 5. Ovigerous female (l) dorsal, (m) lateral. Scales represent 1 mm.

D. curallii sp. nov. is the first species of the genus *Dynamene* to be recorded for sub-tropical and tropical habitats in the Southern Hemisphere. In the Northern Hemisphere only *D. edwardsi* has been recorded from within the tropics.

During the present study it was noted that in the two Australian species the coxal plates of pereonite 7 of the adult males have smoothly rounded posterior margins. This contrasts markedly with the strongly bidentate margins found in all the Afro-European species and clearly separates the two geographical groups. Males of *D. ramuscula* can easily be separated from those of *D. curallii* by the structure of the pleotelsonic ornamentation and pereonal spines, and by the absence of a tubercle on the postero-lateral tergal margin of pereonite 6 of *D. curallii*. Other factors separating the two species are: the shape of the epistome (that of *D. ramuscula* being acute and that of the new species being transverse); the relative width of that region of the cephalosome lying between the antennular bases (that of *D. ramuscula* being proportionally much narrower than that of the new species); and the relative lengths of the postero-ventral pleotelsonic shelf (that of *D. ramuscula* being proportionally shorter than that of the new species).

Dynamene is a common component of the epifauna of seaweeds and the infauna of rock crevices, empty barnacle tests and sponges in the Mediterranean and adjacent seas and on the Atlantic coasts of Western Europe and NW. Africa. In its reproductive habitat at least it has few isopod competitors. However, in other geographical locations its intertidal niche is often filled by *Dynamenella* spp. This is also the case on the Queensland mainland coast and in the intertidal zone of continental islands, such as Lizard Island. Three species of *Dynamenella* were found (Holdich, unpubl. obs.) associated with the rocky intertidal zone on Lizard Island but *D. curalii* was only found associated with the coral reef. On Heron Island, however, where the bulk of the intertidal zone is composed of coral, *Dynamenella* was restricted to the upper eulittoral beach rock.

The apparent discontinuous geographical distribution of *Dynamene* may not in fact be so marked now that it is known that some members of this genus occupy coral habitats. More intensive collecting is needed in the Indo-Pacific coral habitat to show whether this is the case or not.

ACKNOWLEDGMENTS

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A NEW TAENIACANTHID COPEPOD FROM THE ESOPHAGUS OF A SEA URCHIN IN QUEENSLAND

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ABSTRACT

The cyclopoid copepod *Clavisodalis salmacidis* sp. nov., the fifth taeniacanthid to be reported from sea urchins, occurs in the esophagus of the temnopleurid *Salmacis belli* Döderlein in Queensland. The new species may be distinguished from its only congener by the female genital segment being about as long as wide, the caudal ramus separated from the anal segment, and the claw of the female maxilliped unguiform and recurved with two rows of spines on its attenuated tip, the claw of the male maxilliped terminating in a spinulose area.

Four taeniacanthid copepods have been described from Echinoidea. Humes and Cressey (1961) described three species from *Diadema setosum* (Leske) in Madagascar — *Echinosocius pectinatus, Echinosocius dentatus,* and *Echinirus laxatus.* Humes (1970) described *Clavisodalis heterocentroti* from *Heterocentrotus trigonarius* (Lamarck) at Eniwetok Atoll. In addition, Gooding (1965) found two more species of *Echinosocius* and another species of *Echinirus* living with *Diadema* at Singapore, but did not describe them. Other taeniacanthids occur on fishes.

The dissection of three Aristotle's lanterns of *Salmacis belli,* preserved in alcohol, revealed the copepods which are the subject of this paper. The copepods were found clinging by means of the second antennae to the lining of the esophagus.

MATERIALS AND METHODS

The copepods were cleared in lactic acid. Dissections were prepared using the method described by Humes and Gooding (1964).

The figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are: A_1 = first antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, and P_{1-4} = legs 1–4.

Family TAENIACANTHIDAE Wilson, 1911
Genus **Clavisodalis** Humes, 1970

Clavisodalis salmacidis sp. nov.
(Figs. 1–42)

MATERIAL EXAMINED

HOLOTYPE: QM W7977, ♀, from oesophagus of *Salmacis belli* Döderlein, trawled in Moreton Bay, SE Queensland, by C. Boel, 25.v.1977.

PARATYPES: QM W7978, ♂, allotype, same data as holotype. QM W7979, 3 ♂, 5 ♀, QM W7980, 9 copepodids, same data as holotype. One ♂, 2 ♀, in the collection of the author (dissected).

DESCRIPTION

FEMALE: Body (Figs. 1, 2) elongate and moderately flattened, dorsoventral thickness of prosome about 0·47 mm. Length (not including setae on caudal rami) 2·07 mm (1·98–2·24 mm) and greatest width 0·68 mm (0·62–0·73 mm), based on four specimens in lactic acid. Segment of leg 2 almost completely fused with segment of leg 1; slight separation seen only in lateral view (Fig. 2). Anterior part of prosome guitar-shaped in dorsal view and wider than succeeding segments. Ratio of length to width of prosome 2·25:1. Ratio of length of prosome to that of urosome 2·34:1.

Segment of leg 5 (Fig. 3) 130 × 234 μm. Genital segment 260 μm long, in dorsal view expanded in its anterior half (width 263 μm) and with nearly parallel sides in its posterior half (width 164 μm). Genital areas situated laterally on expanded part. Each area (Fig. 4) with three smooth setae 75, 37, and 10 μm long. Three postgenital segments from anterior to posterior 101 × 148, 55 × 140, and 75 × 166 μm. Anal segment with lateroventral row of spinules on both sides (Fig. 6).

Caudal ramus (Figs. 5, 6) moderately elongate, 127 × 68 μm, ratio of length to width 1·87:1. Outer lateral seta 51 μm and dorsal seta 40 μm, both smooth. Outermost terminal seta 78 μm, innermost terminal seta 75 μm, and two median terminal setae 180 μm (outer) and 300 μm (inner), all with small lateral barbules. Ventral row of spinules near insertion of outermost terminal seta. Left caudal ramus of one female lacking dorsal seta and having extra row of spinules near outermost terminal seta (Fig. 7).

Body surface smooth with very few hairs (sensilla).

Egg sac (Figs. 1, 8, 9, 10) with 3–14 eggs, each about 170 μm in average diameter. Largest egg sac seen (Fig. 10) 0·74 × 0·40 mm, with 14 eggs.

Rostral area (Fig. 11) broad and projecting slightly anteriorly.

First antenna (Fig. 12) 323 μm long and 5-segmented. Lengths of segments (measured along their posterior nonsetiferous margins): 73 (143 μm along anterior margin), 75, 44, 35, and 26 μm respectively. Formula for armature: 19, 8, 4, 2 + 1 aesthete, and 7 + 1 aesthete. Many setae on first segment with short barbules; setae on segments 2–5 smooth.

Second antenna (Figs. 13, 14) 3-segmented, with formula 1, 1, 7 (terminally with three clawlike spines and three setae and subterminally with a very small seta). Seta on second segment with truncate, very finely denticulate tip. Third segment ornamented on its inner surface with spinules. Distal outer corner of segment produced to subacuminate point and bearing row of spinules and small setiform element. One of three terminal spines strongly recurved (Fig. 15).

Maxillary hook (Fig. 16) elongate and slender, 118 μm along shorter side, 156 μm along longer side.

Labrum (Fig. 17) with broadly rounded posteroventral margin bearing row of spines. Mandible (Fig. 18) terminally with stout unilaterally pectinate spine and adjacent small spiniform process. Paragnath (Fig. 17) a small smooth lobe. First maxilla (Fig. 19) with three setae. Second maxilla (Fig. 20) 2-segmented, second segment having terminally two stout spines with strong lateral spinules and one small naked seta. Maxilliped (Figs. 21, 22) 3-segmented. First segment elongate and unarmed. Second segment small and wedge-shaped. Third segment forming a recurved claw 125 μm long with prominent subterminal spinules and bearing proximally an antero-outer seta and two very small postero-inner setules. Arrangement of mouthparts as in Figure 23.

Ventral area between maxillipeds and first pair of legs without special sclerotization.

Leg 1 (Fig. 24) with both rami 2-segmented. Legs 2–4 (Figs. 26, 29, 30) with 3-segmented rami. Formula for armature (Roman numerals representing spines, Arabic numerals indicating setae) as follows:

P_1: coxa 0–0, basis 1–1, exp. I–0;8, enp 0–1;7.

P_2: coxa 0–0, basis 1–0, exp I–0;I–1;II,I,3, enp 0–1;0–1;I,I,3.

P_3: coxa 0–0, basis 1–0, exp I–0;I–1,I,1,I,2,1, enp 0–1;0–1,I,2.

P_4: coxa 0–0, basis 1–0, exp I–0;I–1;I,1,3,1, enp 0–1;0–1;1,3.

Legs 1 and 2 with intercoxal plates bilaterally armed with spines on free margin. Leg 1 (Fig. 24) with basis having strong spines along inner and inter-ramal margins; these inter-ramal spines absent in legs 2–4. Inner lobe of basis with barbed seta; this seta absent in legs 2–4. Second segment of exopod with eight setae as in Figure 25, but rarely with seven setae as in Figure 24. Leg 2 (Fig. 26) with outer spine on first segment of exopod bearing spines on posterior surface (Fig. 27). One female with both rami of leg 2 abnormal as shown in Figure 28. Leg 3 (Fig. 29) with outer side of third segment of exopod bearing I, 1, I. Leg 4 (Fig. 30) with hairs on outer margin of first and second segments of endopod.

Leg 5 (Fig. 31) 2-segmented. First segment approximately 52 × 47 μm, with seta 45 μm, and bearing ventrodistally a row of fine spinules. Second segment elongate, 114 × 44 μm, bearing four distal setae 39, 39, 127, and 88 μm, all minutely barbed. Row of very small spinules along distal end of segment.

Leg 6 probably represented by three setae on genital area (Fig. 4).

Color unknown.

MALE: Body (Fig. 32) resembling in general aspects that of female. Length (excluding setae on caudal rami) 1·50 mm (1·40–1·57 mm) and greatest width 0·58 mm (0·55–0·61 mm), based on seven specimens in lactic acid. Segment of leg 2 separated from segment of leg 1 by dorsal transverse suture. Ratio of length to width of prosome 1·58:1. Ratio of length of prosome to that of urosome 1·52:1.

Segment of leg 5 (Fig. 33) 86 × 213 μm. Genital segment 135 × 221 μm, subrectangular and wider than long. Genital areas located laterally near posterior margin of segment (Fig. 42). Three postgenital segments from anterior to posterior 114 × 164, 99 × 151, and 107 × 122 μm.

Caudal ramus (Fig. 33) similar to that of female, but smaller, 104 ×49 μm. One male with abnormal caudal rami (Fig. 34).

Body surface smooth, with very few sensilla as in female.

Rostral area, first antenna, second antenna, maxillary hook, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 35) massive, 4-segmented. First segment short with one smooth seta. Large second segment swollen proximally, bearing on inner less swollen side two small setae and five prominent spines and other smaller spines as indicated. Small third segment unornamented. Fourth segment forming a stout, slightly recurved claw bearing four proximal setae, longest of them minutely barbed, and having on anterior surface a row of delicate spinules leading toward finely spinulose tip (Fig. 36).

Ventral area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented and armed as in female, with same spine and setal formula. Leg 1 (Fig. 37) with certain setae having several long proximal hairs, a few of these setae plumose rather than with short barbs. Leg 2 resembling female but terminal spine on exopod with blunt tip and naked throughout except for minute spinules near tip (Fig. 38), and endopod (Fig. 39) with outer hairs on second segment. Leg 3 similar to that of female, but terminal spine on exopod with blunt tip as in leg 2. Left endopod in one male with abnormal armature (Fig. 40), right endopod in this male normal. Leg 4 like that of female, but one male with abnormal endopods (Fig. 41).

Leg 5 (Fig. 42) resembling that of female. First segment 39 x 34 μm and second segment 91 x 36 μm.

No setae visible on genital area and leg 6 apparently absent.

Extruded spermatophore not seen.

Color unknown.

ETYMOLOGY: The specific name *salmacidis* is the genitive form of the generic name of the host, from Σαλμακις, a nymph who in the fountain of Caria embraced a youth named Hermaphroditus, and both grew together.

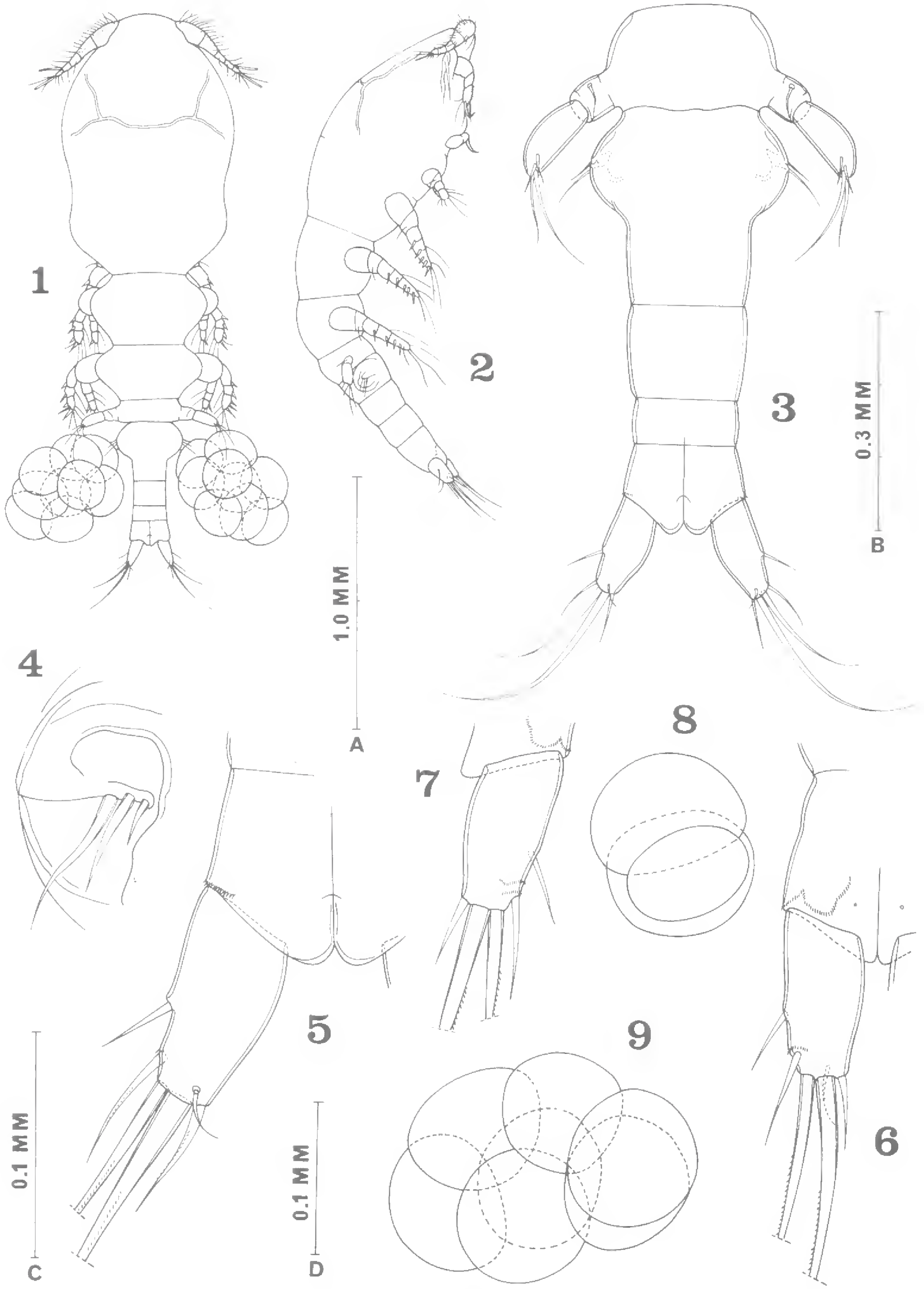
DISCUSSION

Clavisodalis salmacidis differs from *Clavisodalis heterocentroti* in several features easily seen without dissection in animals cleared in lactic acid. These selected characters are shown in Table 1.

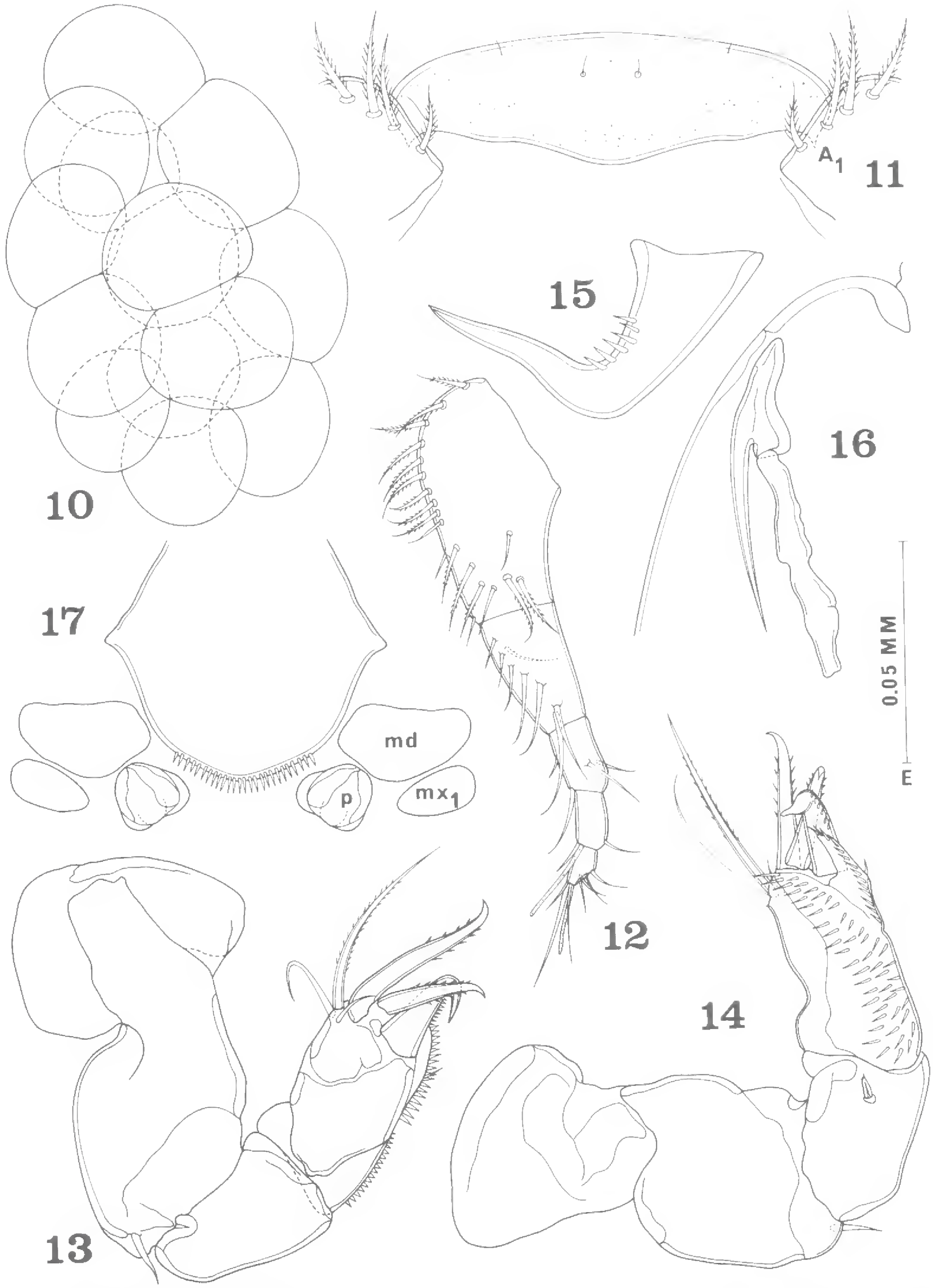
In both *C. heterocentroti* and *C. salmacidis* the armature of legs 1–4 is subject to variation. Most individuals, however, conform to the formula as indicated for the two species respectively. Accurate identification obviously requires observation of more than one copepod.

TABLE 1: CHARACTERS USEFUL FOR THE DIFFERENTIATION OF THE TWO SPECIES OF *CLAVISODALIS*.

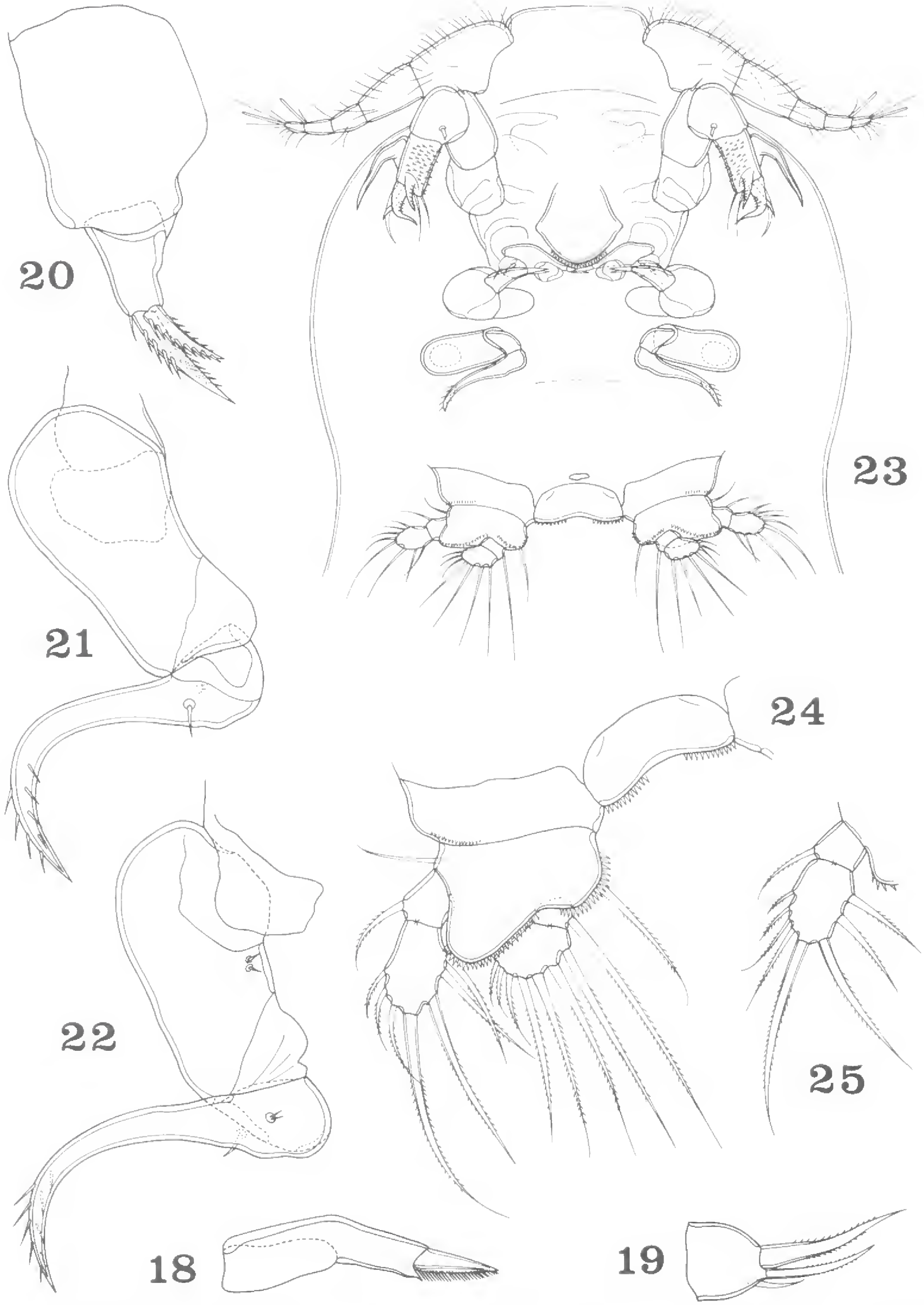
Character	*C. heterocentroti*	*C. salmacidis*
FEMALE		
genital segment	much wider than long	about as long as wide
caudal ramus	fused with anal segment	separated from anal segment
claw of maxilliped	clavate, not recurved, with cluster of spines on blunt tip	unguiform, recurved, with two rows of spines on attenuated tip
number of setae on second segment of P_1 Exp and Enp	7, 6	8, 7
armature of segments 1 and 2 of P_3 and P_4 Enp	0–0; 0–0	0–1; 0–1
armature of inner side of second segment of P_4 Exp	none	one seta
MALE		
claw of maxilliped	terminating in fine filament	tip with spinulose area



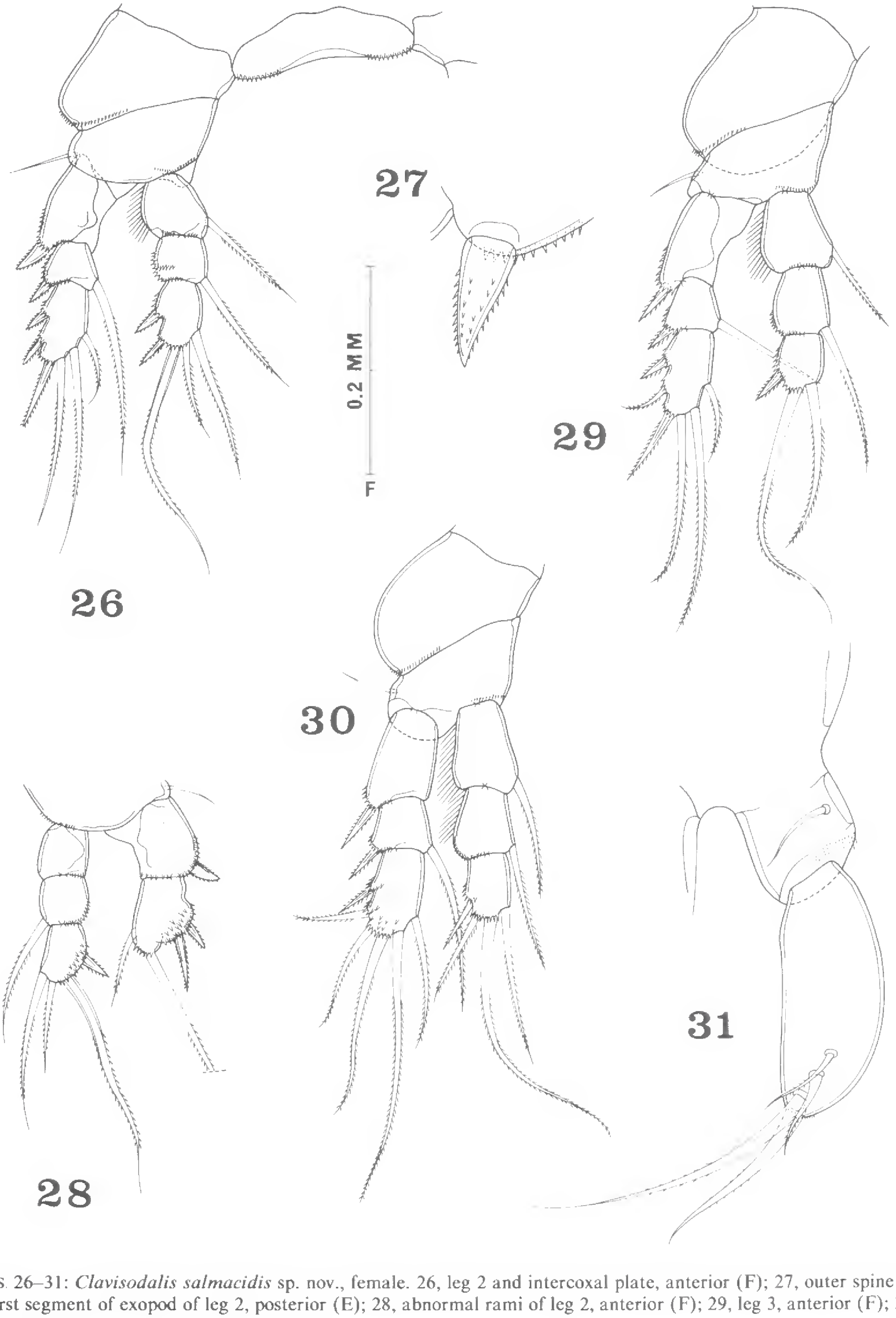
FIGS. 1–9: *Clavisodalis salmacidis* sp. nov., female. 1, dorsal (A); 2, lateral (A); 3, urosome, dorsal (B); 4, genital area, lateral (C); 5, caudal ramus, dorsal (D); 6, caudal ramus, ventral (D); 7, abnormal caudal ramus, ventral (D); 8, egg sac, ventral (B); 9, egg sac, ventral (B).



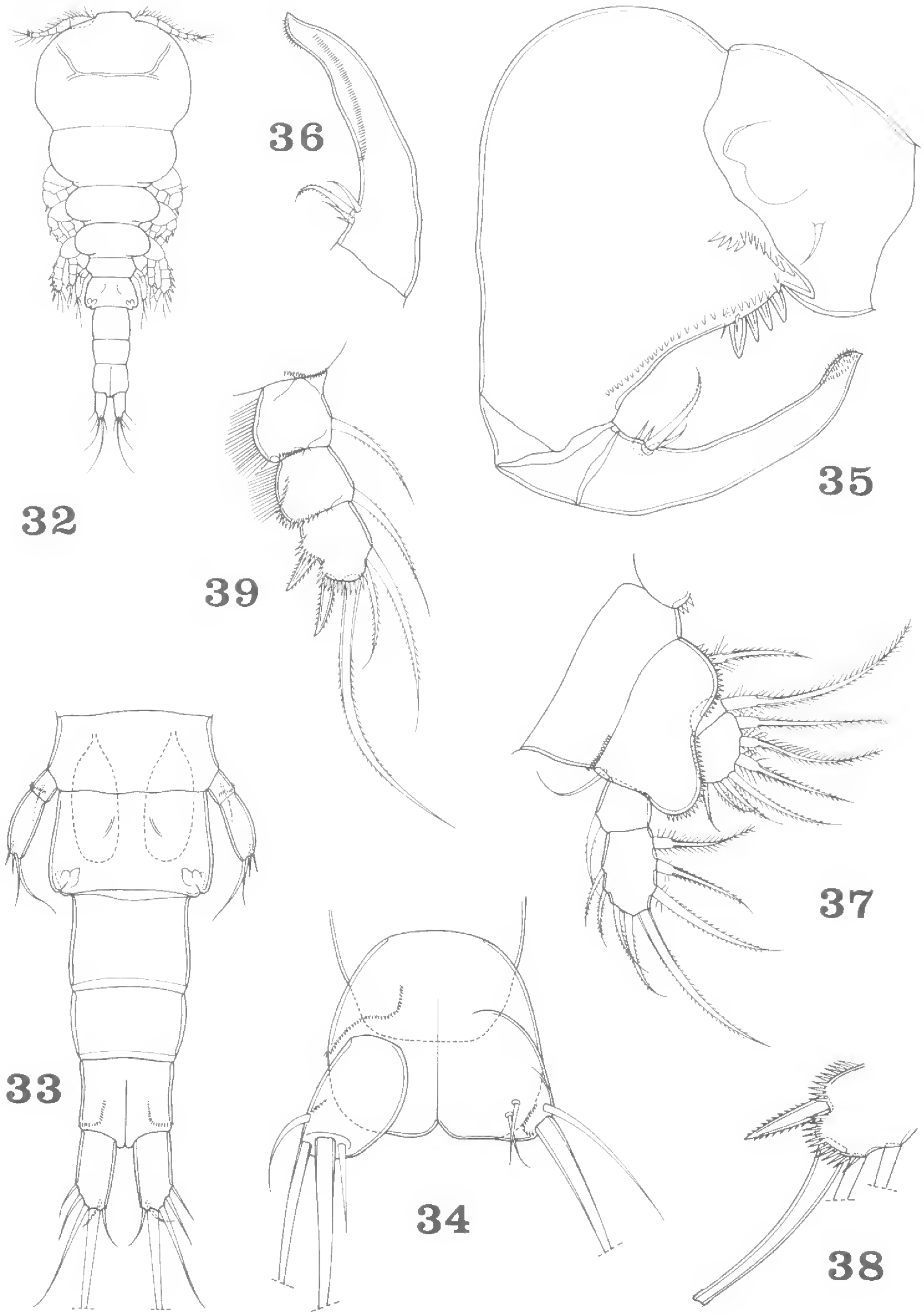
FIGS. 10–17: *Clavisodalis salmacidis* sp. nov., female. 10, egg, sac, ventral (B); 11, rostrum, ventral (C); 12, first antenna, ventral (D); 13, second antenna, outer (C); 14, second antenna, inner (C); 15, terminal spine on second antenna, posterior (E); 16, maxillary hook, ventral (D); 17, labrum and paragnaths, ventral (C).



FIGS. 18–25: *Clavisodalis salmacidis* sp. nov., female. 18, mandible, ventral (C); 19, first maxilla, postero-inner (C); 20, second maxilla, postero-inner (C); 21, maxilliped, antero-outer (C); 22, maxilliped, postero-inner (C); 23, cephalosome, ventral (B); 24, leg 1 and intercoxal plate, anterior (D); 25, exopod of leg 1, anterior (D).



FIGS. 26–31: *Clavisodalis salmacidis* sp. nov., female. 26, leg 2 and intercoxal plate, anterior (F); 27, outer spine on first segment of exopod of leg 2, posterior (E); 28, abnormal rami of leg 2, anterior (F); 29, leg 3, anterior (F); 30, leg 4, anterior (F); 31, leg 5, dorsal (C).



FIGS. 32–39: *Clavisodalis salmacidis* sp. nov., male. 32, dorsal (A); 33, urosome, ventral (B); 34, abnormal anal segment and caudal rami, ventral (D); 35, maxilliped, postero-inner (C); 36, claw of maxilliped, anterior (C); 37, leg 1, anterior (D); 38, terminal spine on exopod of leg 2, anterior (C); 39, endopod of leg 2, anterior (D).

The site of taeniacanthid copepods in sea urchins appears to be the esophagus. This is confirmed by the recovery of *C. salmacidis* from the esophagus and by information supplied by Gooding (personal communication to the author) that such copepods are commonly to be found at this site in tropical Pacific Echinoidea. When taeniacanthids were first discovered in 1955 in *Diadema* in Madagascar, they were obtained by washing the entire urchins in sea water with 5 per cent ethyl alcohol. This undoubtedly stimulated some of the copepods to crawl from the esophagus out of the mouth. They were subsequently recovered from the sediment resulting from the washing. Many more copepods could perhaps have been found if the esophagus of each urchin had been opened. Unfortunately, at that time it was not known that the real habitat of these copepods is the esophagus.

The range of the host urchin, *Salmacis belli*, extends throughout the East Indies and North Australia (Clark and Rowe 1971). At present *Clavisodalis salmacidis* is known only from southeastern Queensland. Whether the copepod follows the range of the host is not known.

ACKNOWLEDGMENTS

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I am greatly indebted to Dr L.R.G. Cannon, Queensland Museum, for sending me the Aristotle's lanterns and allowing me to remove the copepods for study.

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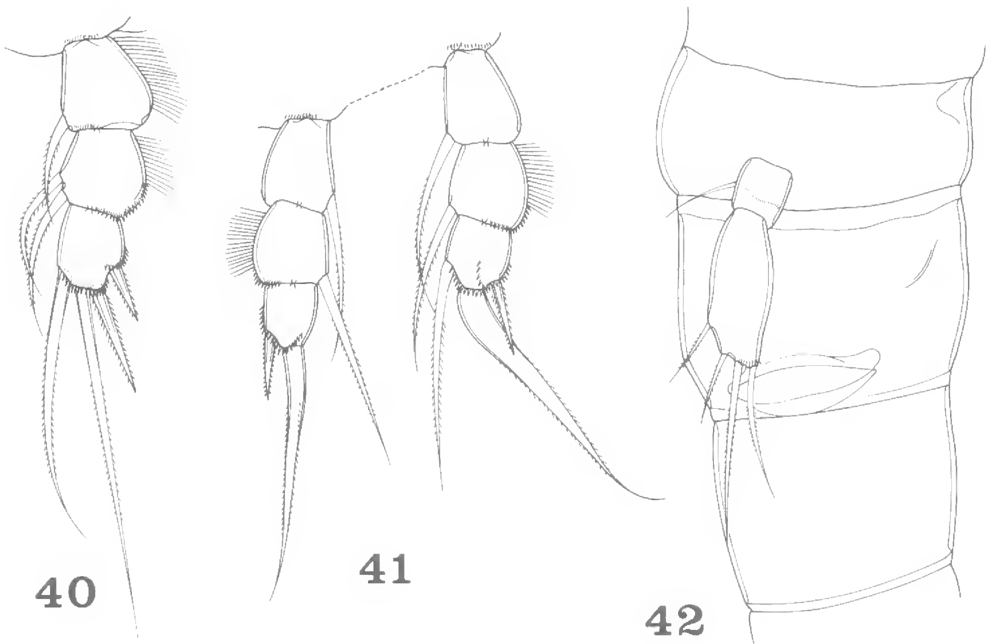

Figs. 40–42: *Clavisodalis salmacidis* sp. nov., male. 40, abnormal endopod of leg 3, anterior (D); 41, abnormal endopods of leg 4, anterior (D); 42, segment of leg 5, genital segment, and first postgenital segment, lateral (D).

Mem. Qd Mus. **20**(1) 181–235, pls. 1–16 [1980]

A REVISION OF THE CORAL GENUS *LEPTOSERIS* (SCLERACTINIA: FUNGIINA: AGARICIIDAE)

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ABSTRACT

Seventeen of the 28 nominal recent species of *Leptoseris* are placed in synonymy. The remaining seven Indo-Pacific species and two species from the Caribbean region are redescribed, and two new species found in Great Barrier Reef waters, *Leptoseris foliosa* and *Leptoseris glabra*, are described. History, ecology, and zoogeography of the genus are discussed.

The scleractinian genus *Leptoseris* has seldom been treated in any depth in taxonomic works. Although widely distributed geographically, it is a comparatively uncommon coral; it never occurs on reef flats, usually prefering deep water or shaded conditions. Hence it is poorly represented in museum collections and most previous workers have had at their disposal only small suites of specimens. Consequently, they have not appreciated the range of variation exhibited by some species.

The aim of this study is to provide a revision covering all recent species of *Leptoseris*. To this end many hundreds of specimens were collected, by SCUBA diving, from Great Barrier Reef waters, principally from the central region of the Great Barrier Reef, from the Lizard Island region, and the Palm Islands. Information about the living colonies, and their habitat, was recorded. I have also examined numerous specimens from a variety of Indo-Pacific and West Indian localities, including nearly all available type specimens, and other museum specimens referred to in the literature.

The large series available for most species demonstrated considerable variability in some species, and seventeen of the 28 available names are shown to be synonyms. I recognise 11 recent species, seven of which occur in the Great Barrier Reef region.

TAXONOMIC HISTORY

Initially species were assigned to existing genera; subsequently several genera were created to accommodate the various species. This confusion persisted because of the variety of growth forms found within the genus. *Leptoseris papyracea* (Dana), for example, was originally placed in several different genera.

INDO-PACIFIC SPECIES: The first described species of *Leptoseris* is apparently *Agaricia crispa* Ehrenberg, 1834. Dana (1846) moved Ehrenberg's species to *Pavonia*, and added *P. papyracea*, although the descriptions suggest that these two species are probably synonymous. The genus *Leptoseris* was established in 1849 by Milne-Edwards and Haime who did not attribute to the genus the small branching species now recognised as *Leptoseris*; their 1851 description (p. 133) is as follows: 'Polypier composé et adhérent. Plateau commun, nu, délicatement strié, s'élevant de façon à constituer un disque subcrateriforme, dont le centre est occupé par un individu parent et entoure par de plus petits. Calices très imparfaitement circonscrits, mais bien radiés; rayons cloisonnaires très longs. Columelle tuberculeuse.

La *Leptoseris* est très voisine des Mycédies, mais elle nous paraît devoir en être distinguée à cause de la diffluence des calices qui sont toujours fort rares, et de la grande étendue des rayons septo-costaux.'.

Milne-Edwards and Haime (1849, 1851) also described the genus *Haloseris* in which they placed Ehrenberg's *crispa*, but not Dana's species *papyracea*. Their rather brief description of *Leptoseris* led Rousseau (1854) to include in it *Leptoseris edwardsi*, which is in fact a *Lithophyllon* (see Wells 1966).

Duncan (1884) listed *Leptoseris*; however, he relegated *Haloseris* to a subgenus of *Lophoseris*

(=*Pavona*). Quelch (1886) described two new genera — *Cylloseris* with its numerous hydnophoroid projections (it is not surprising that he did not recognise in it the *Leptoseris* of Milne-Edwards and Haime) and *Domoseris* which he admitted (p. 125) 'somewhat resembles *Leptoseris* at the extreme marginal parts'.

Bassett-Smith (1890) considered Dana's *papyracea* referrable to *Pavonia* rather than to *Leptoseris* and described two further species, *P. pretiosa* and *P. ramosa*, both synonyms of *L. papyracea*. However Rehberg (1892) established the genus *Folioseris* in which he placed both *papyracea* and the *crispa* of Ehrenberg (but not *H. crispa* of Milne-Edwards and Haime because of its lack of columella). But his own specimens of *F. papyracea* are not the same as Dana's species and are synonymous with *L. gardineri* van der Horst!

Gardiner (1905) doubted whether *Domoseris* was distinct from *Leptoseris*, but clearly considered *Cylloseris (C. incrustans)* separate, for he described *L. incrustans* as a new species. Vaughan (1907) similarly questioned the validity of *Domoseris*, and placed *Folioseris* in synonymy with *Leptoseris*. Like Vaughan, van der Horst (1921) felt that *Folioseris* and Dana's *papyracea* belonged in *Leptoseris*, and he recognised that Quelch's *Cylloseris* is also a *Leptoseris*.

Although Vaughan (1918) and Faustino (1927) placed both papyracea and its synonym *L. digitata* Vaughan in *Leptoseris*, they both retained *Haloseris* as a separate genus. Finally, Yabe, Sugiyama, and Eguchi (1936) referred several specimens of a *Leptoseris* species typified by the presence of collines and (often) lacking 'normal' *Leptoseris* corallites to *Agaricia* (?) *minikoiensis*, mistakenly believing them to be the same as Gardiner's (1905) *Agaricia ponderosa* var. *minikoiensis*. Ma (1937) instead placed these specimens in a new subgenus, *Agaricia* (*Agariciella*), but gave no reasons in the text. Wells (1954) described this species as *Leptoseris? mycetoseroides* and included in synonymy the Japanese specimens.

ATLANTIC SPECIES: *Madrepora cucullata* was described by Ellis and Solander in 1786. Milne-Edwards and Haime (1849) made this the type of a new genus, *Helioseris*, but later (1851) submerged this in *Mycedium*. Wells (1956) considered *Helioseris* a synonym of *Leptoseris* but subsequently (1973) re-established the genus because of its lack of a columella. However, since some specimens have a distinct columellar structure, there seems to be no good reason for retaining *Helioseris* as a separate genus, and the species *cucullata* is now included in *Leptoseris*. A second Caribbean species, *Mycedium cailleti* Duchassaing and Michelotti, 1864, was retained in *Mycedium* by Pourtalès (1874), but because of the species' obvious agariciid characters, subsequent authors (Vaughan 1901, Porter 1972, Wells 1973) referred the species to *Agaricia*. This species is here included in *Leptoseris*, as it seems much more closely allied to other species of that genus than to any *Agaricia*.

Thus in accordance with Vaughan and Wells (1943), and Wells (1956) I include *Haloseris*, *Helioseris*, *Cylloseris*, *Domoseris*, and *Folioseris* in *Leptoseris* adding Ma's *Agariciella* as did Wells (1956).

ECOLOGY AND ZOOGEOGRAPHY

Several species of *Leptoseris* may be found in soft bottom areas (coarse sand to mud) living apparently free, or attached to a piece of substrate such as coral rubble. The genus also occurs unshaded on solid substrate, and in crevices, caves, and overhangs. It may grow in conditions of strong current but very rarely in high energy situations with waves or surf. It can occur as deep as 470 m (Vaughan 1907) and plays a significant role in the deeper hermatypic communities. Wells (1954), in his description of the seaward slope of Bikini Atoll, defines the *Leptoseris* zone as 91–146 m, below the *Echinophyllia* zone but above the ahermatypic *Sclerhelia–Dendrophyllia* zone. At Bikini these zones may be more clearly defined than usual and also deeper than usual because of extreme water clarity. But there is no doubt that *Leptoseris* is important in coral communities occurring below the normal hermatypic range, and subsequent records confirm this view. (See, for example, Barnes *et al.* 1971, Pichon 1973, Dinesen 1977.)

Leptoseris is a coral of fairly restricted habitat, and its contribution to reef structure is limited. However, in soft bottom areas with large stands of *L. gardineri*, and an abundance of *L. glabra* and *L. scabra*, it may be a dominant coral in a strictly local sense. Furthermore, in some Outer Barrier situations (especially in channels and some back reef patches) which are favourable for growth of *Leptoseris*, large colonies of several species are not uncommon. Their contribution to the total coral cover is of some significance.

Five Australian species (*L. hawaiiensis*, *L. glabra*, *L. mycetoseroides*, *L. papyracea*, and *L. scabra*) have been tested for the presence of

zooxanthellae, and all tests have proved positive. It is likely that all *Leptoseris* species are hermatypic, though quite possibly some deep-living specimens may lack zooxanthellae. The preference of many *Leptoseris* species for deep water or shady conditions may be due to an inability to tolerate too much light, or to competitive exclusion, or both. Specimens of *Leptoseris* have been found in shallow water in gullies, exposed to strong sunlight but only for limited periods. This observation suggests that if *Leptoseris* is sensitive to over-illumination, it is not the light intensity itself but rather the time of exposure to strong light that has an adverse effect.

The distributions of the various species are given following each description. The records indicate that *Leptoseris* is widely distributed in the Indo-Pacific but less well represented in the Caribbean region. Definite records for some species may be widely spread geographically, but it seems reasonable to assume that many of these species do occur throughout much of the Indo-Pacific, and could be found if sought in the right biotopes.

From available data, two species (*L. incrustans* and *L. solida*) are confined to the eastern or eastern and central Pacific, and *L. foliosa* to the western Pacific. Few collections have been made of *L. cailleti*, all from localities broadly scattered in the Caribbean area. There has been little mention of *L. cucullata* in the literature, but Wells (1973) reported that it is not uncommon throughout the West Indies in depths below about 8 m.

Terminology

The terminology followed is basically that given by Moore, Hill, and Wells (1956). The specific use of the following terms should be noted.

'Septocostae' is used as defined by Duncan (1884, p. 201): 'The costae may be directly continuous with the septa at the calicular margin, and may pass from calice to calice. Where there is continuity, the costae are termed septocostae.' Although some workers may refer to the continuation of septa between centres as 'costae', it seems traditional in the *Leptoseris* literature to call these 'septocostae'. In a genus where a distinct mural structure is generally lacking, the point at which a septum becomes a septocosta may be somewhat arbitrary. Here 'septum' denotes that part of the structure which lies within what is judged to be the thecal rim. The term 'costae' is reserved for the striations on the non-calicinal surface.

'Septal profile' denotes the shape of the septal margin as septa drop into the fossa. The 'upper margin profile' of the septocostae is the shape of the septocostal margin in section, e.g. rounded or acute. 'Surface ornamentation' refers to the granulations visible under the lens on the surface of the septa and septocostae. This includes 'lateral ridges', which may be set in rows on the sides of septa and septocostae, parallel to the upper margin.

The 'fossa' ('calicular axial fossa', Duncan 1884, p. 201) is the axial depression in a calice, usually partly filled by the columella, here considered to be demarcated by the inner ends of the septa. Some species typically have corallites which are inclined towards the corallum margin. In such cases the inner or proximal side of a corallite will be raised into a cushion-like structure, here termed 'proximal cushion'.

Methods

Field Methods: Material was collected by SCUBA diving. Details of depth and general habitat were always recorded; colour, growth form of entire living colonies, and microhabitat (e.g. position in a cave) were usually recorded. Some specimens encountered in caves (where indentifiable in the field) were not collected.

Laboratory Methods: Specimens were cleaned in a solution of sodium hypochlorite. Material was examined with a Nikon SMZ-2 binocular microscope, and measurements (apart from corallum size) were taken using an eyepiece with a square grid graticule. Where only a small suite was available for a species, measurements were taken from all material. With larger series, a proportion of representative specimens (20–40 per cent) was measured and examined in detail. Remaining material was checked over and all major features noted. In general, at least four measurements were made of each character on a specimen, and rather more measurements were made of septal number, size of corallites and fossae, and thickness of septocostae. Emphasis has been placed on those characters most useful in distinguishing the species.

Measurement of Characters: For most measurements, the range is given first, followed by the mean or usual figure in parenthesis — e.g. corallites 1·0–5·0 mm (2·0–3·0 mm) by 1·0–4·0 mm (2·0–2·5 mm).

Corallum: In general, only the dimensions of the largest coralla examined are given. These are listed as length in the larger diameter followed by the maximum width at right angles to this. Height is sometimes indicated in the case of erect colonies.

Corallites: In the absence of a well defined thecal rim (e.g. in *L. foliosa*), it is difficult to give precise measurements of corallite size. In such cases, measurements should be treated as a guide only. Since corallites are often elliptical, the length of the greater axis is normally given first, followed by that of the shorter axis. The distance between corallites or rows of corallites was measured between fossae. Only a radial measurement is given, i.e. the distance apart parallel to the corallum margin or branch tips.

Septal counts: If corallites are poorly defined, the number of septa per centre may be a somewhat subjective estimate, especially if many new septocostae are inserted in the area surrounding a corallite. For example, in his description of the holotype of *L.? mycetoseroides,* Wells (1954) gives the total septa as 25–35. On the same specimen I was not able to count as many as 35 septa in a calice. Presumably the figure reached depends upon one's estimate of the corallite border. Some *Leptoseris* species have many more septa per centre than others, so that septal number is still a very useful character.

Septocostae: The thickness of septocostae was measured using the grid graticule where each grid square = 0·5 mm. Each square could be approximately divided by eye into quarters, i.e. about 0·125 mm. Measurements are given to two decimal places; where these are quoted as increments of <0·5 mm, they should be considered merely a good estimate. Septal thickness has not been measured because the septa always taper and become thinner towards the centre of the corallite. The maximum septal thickness is never greater than the maximum thickness of the septocostae, and is usually less. Since septocostae tend to be thinner at the corallum margin, measurements were made both at the margin and elsewhere on the corallum.

The number of septocostae in a given distance (5 mm) was most conveniently measured by counting with the grid at right angles to rows of parallel septocostae. For very narrow forms (e.g. *L. papyracea)* septocostae were counted within 2·5 mm, but for consistency these figures have been corrected for a 5 mm distance.

Dentation of septocostal margin: For large dentations, the size of these is indicated. Where dentations are minute, figures are restricted to the number of dentations in a given distance of septocostal margin.

Fossae: Usually the diameter of the longer axis is followed by that of the shorter axis. Depth of fossae is merely estimated (e.g. deep, very shallow).

Costae: For the number of costae in 5 mm, separate counts for the corallum margin were not made. Costal spines, where set in a row, were measured within 1 mm.

Collines, proximal cushions, nodules: The range or maximum size of these structures is indicated, if appropriate.

IDENTIFICATION OF *LEPTOSERIS:* Because *Leptoseris* often occurs in a relatively restricted range of biotopes, there may be less intraspecific variation than in corals which are very widely distributed on reefs (e.g. acroporids and faviids). However, some *Leptoseris* species may vary considerably, both in the general morphology of the corallum and in finer skeletal structure. Much of the variation within the species may be found within a single colony, especially as regards corallite size, septal number and columellar development. Many of the species must be differentiated by taking into account a combination of characters, when material comes close to the species' limits in some characters. Which characters will be most useful in identifying a specimen may depend both on the species in question and on the material itself. For this reason, it is not possible to construct a simple dichotomous key to the species of *Leptoseris*. The inclusion of a more complex key would probably lead to unnecessary confusion. For identification, reference should first be given to the photographic plate, then to the appropriate species descriptions bearing in mind generic characters are not always repeated in individual descriptions.

Certain species of some corals may be more easily distinguished in the field than in the laboratory. (See, for example, Wallace 1978 on *Acropora.)* Although typical specimens of all species of *Leptoseris* can be recognised underwater by the experienced observer, in my experience, problems with the identification of *Leptoseris* are best resolved by examining specimens under the microscope.

The most important characters for distinguishing species are as follows: corallum shape, size and arrangement of corallites, number of septa per centre, and the structure of the septocostae.

SYNONYMY: No synonymies given by other authors have been accepted without investigation. With the exception of *L. cucullata,* the type of which has not been examined, synonymy lists are restricted to material examined by the author or by M. Pichon (of James Cook University), and to specimens which have been clearly illustrated in the literature. For example, Ma (1959) includes a number of plates of *Leptoseris* specimens collected by earlier workers. Only where his figures provide unequivocal illustrations of a species, have they been included in the synonymy.

The holotype of the type species of *Leptoseris, L. fragilis* Milne-Edwards and Haime, appears to have been lost (see note following generic synonymy).

The holotype of *Leptoseris tenuis* van der Horst has also apparently been mislaid. This problem is considered in the discussion section for *L. foliosa.*

BATHYMETRIC RECORDS: The minimum and maximum records are given for specimens collected in Great Barrier Reef waters, but for other material only the maximum record is quoted (except if the species does not occur on the Great Barrier Reef).

DISTRIBUTIONS: Information does not include all records in the literature, but only records for material listed in the synonymy and for specimens examined by the author. Records for unregistered specimens or material received after the species descriptions were written have been included where they increase the geographical range of a species.

MATERIAL EXAMINED: Because a large amount of material is involved, collection details have been summarised. For material from the Great Barrier Reef region, relatively precise locality details are included. All such specimens were collected between 1976 and 1978, mostly by the author, but collector and actual collection dates are not listed. For other material, only the registration number and general locality are given.

Collecting stations from the Lizard Island group have been divided into four areas, as follows. Area 1: Lagoon (protected). Area 2: N. Watson's B. to W. side of N. Pt (fairly protected). Area 3: E. side of N. Pt to N. of Crystal Beach (fairly exposed). Area 4: Crystal Beach to South I. (fairly exposed).

All material listed is in registered museum or university collections. These institutions are listed below, with the abbreviations used in the text.

AHF: Allan Hancock Foundation (University of Southern California)
AM: Zoölogisch Museum, Amsterdam
BM: British Museum (Natural History)
CM: University Museum of Zoology, Cambridge
DB: Discovery Bay, Jamaica
EN: Collection from Enewetak (specimens currently at James Cook University (JCU) but to be moved to Bernice P. Bishop Museum, Hawaii)
GF: Collection of G. Faure (Centre Universitaire, Reunion)
MP: Collection of M. Pichon from Indonesia — Philippines region and Great Barrier Reef (specimens at JCU)
MPIO: Collection of M. Pichon from southwest Indian Ocean (specimens at JCU)
PM: Museum Nationale d'Histoire Naturelle, Paris
QM: Queensland Museum
TWCMS: Tyne and Wear County Council Museum, Sunderland, England
UT: University of Tohoku
UTA: University of Tel Aviv
USNM: United States National Museum
WAM: Western Australian Museum
ZD: Collection of Z. Dinesen (specimens at JCU)

SYSTEMATICS

Family AGARICIIDAE Gray, 1847
Genus *Leptoseris* Milne-Edwards and Haime, 1849

Leptoseris Milne-Edwards and Haime, 1849, p. 72. (Type species *Leptoseris fragilis* Milne-Edwards and Haime, 1849, by monotypy. Published simultaneously with *Haloseris* Milne-Edwards and Haime, 1849, p. 72, and *Helioseris* Milne-Edwards and Haime, 1849, p. 72, and selected as valid name for the genus by Vaughan and Wells, 1943, p. 125.)

Haloseris Milne-Edwards and Haime, 1849, p. 72. (Type species *Haloseris lactuca* Milne-Edwards and Haime, 1849, by monotypy. Placed in synonymy with *Haloseris crispa* (Ehrenberg, 1834) by Milne-Edwards and Haime in their 1851 description.)

Helioseris Milne-Edwards and Haime, 1849, p. 72. (Type species *Madrepora cucullata* Ellis and Solander, 1786, by monotypy.)

Cylloseris Quelch, 1886, p. 124. (Type species *Cylloseris incrustans* Quelch, 1886, by monotypy.)

Domoseris Quelch, 1886, p. 125. (Type species *Domoseris solida* Quelch, 1886, so designated in this revision.)

Folioseris Rehberg, 1892, p. 26. (Type species *Agaricia crispa* Ehrenberg, 1834, so designated in this revision.)

(*Agariciella*) Ma, 1937, p. 149. (Type species *Leptoseris mycetoseroides* Wells, 1954 [misidentified by Ma as *Agaricia* (*Agariciella*) *minikoiensis* Gardiner 1905] by monotypy.)

The holotype of *Leptoseris fragilis* Milne-Edwards and Haime, 1849, appears to have been lost. The specimen in the Paris Museum which is supposed to be the holotype is a *Coscinaraea*, and does not fit the description given by Milne-Edwards and Haime (in 1851). Chevalier (1961) redescribed *L. fragilis* from a specimen which he stated was the 'genotype'. Since Chevalier's description is consistent with that of Milne-Edwards and Haime, I assume that Chevalier then had before him the true type specimen. There being no evidence that the true holotype is not a *Leptoseris* (according to the present understanding of the genus) it seems preferable to retain the name *Leptoseris*, than to abandon it in favour of a little-known synonym.

In their description of *L. fragilis*, Milne-Edwards and Haime describe small specimens with distinct central corallites, which might be young *L. hawaiiensis*, *L. scabra* or *L. glabra*. Subsequent authors have referred juvenile examples of more than one species to *L. fragilis*. Thus although *L. fragilis* is given as the type species of the genus, it has not been possible to give this species further consideration in this revision.

I have not been able to obtain the holotype of *Agaricia crispa* Ehrenberg, 1834, from the Berlin Museum. A photograph supplied by the museum is inscribed "*Haloseris crispa* Ehrenberg Philippinen? Kat. Nr. 820". However, the photographed specimen, while clearly a *Leptoseris*, appears larger than that described by Ehrenberg, and rather resembles *Leptoseris cailleti* Duchassaing and Michelotti, a Caribbean species. I am therefore in doubt as to whether the photograph is of the type specimen. It seems very likely that Ehrenberg's *crispa* is a *Leptoseris* (and judging from the literature, probably synonymous with *L. papyracea* (Dana, 1846)). Thus while reference is given to this species in the generic synonymy, it could not be further considered for species synonymies.

Description

Corallum: Colonial, colony formation by circumoral then marginal budding. Growth form encrusting, explanate, bowl-shaped, tubuliferous, fan-shaped or branching. Corallum unifacial, but the margin may be reflected over onto the non-calicinal surface. Size from a few centimetres to about 0·5 m; stands of *L. gardineri* may be several metres across. Colour: beige, brown, green, dark red, mauve, grey, either uniform, or patchy with more than one colour. Sometimes a white margin; occasionally centres and septocostae of contrasting colour. Polyps apparently very small, with few, short, pointed tentacles.

Corallites: Round or elliptical, from 1·0 mm across, up to 12·0 mm in the longer axis of elliptical corallites. Longer axis usually parallel to corallum margin or branch tips. Corallites flush, slightly sunken, or better delineated, with raised rims and directed upwards or towards corallum margin. Scattered or in roughly concentric rows parallel to corallum margin, with 2->30 centres per row. Parent corallite sometimes distinguishable; corallites or rows adjacent or up to several centimetres apart. Proximal cushions, where present, up to 6 mm high, and raised nodular areas up to 8 mm above general corallum surface. Hydnophoroid projections, where present, up to 4 mm high and 7 mm long at base. Collines, if developed, as concentric ridges or intersecting so as to enclose 1–12 centres. Collines 1–5 mm thick at base, up to 8 mm high.

Septa: Equal to strongly alternating, with first order thicker and more exsert. Rarely divisible into cycles. Profile rounded or acute, and variable according to orientation of corallites. Septa taper to become thinner at centre of corallites. Margin smooth or slightly uneven, but not dentate. Usually imperforate. Number per centre: 6–50.

Septocostae: Equal to strongly alternating, with the first order thicker and more exsert. Straight, slightly flexuous, or very contorted. In coralla with branches which become wider towards the tip, septocostae may form a diverging, fan-like pattern as septocostae become more numerous higher up the branches. Upper margin profile rounded, acute, or flattened with a narrow ridge running down centre. Margin smooth; with long, wave-like undulations, 0·5–2·5 mm long; with minute dentations, 3–10 in 1 mm; or with large, often peg-like dentations, 6–18 in 5 mm. Septocostae perforate or imperforate. Thickness: <0·13–1·0 mm. Number in 5 mm: 11–36.

Surface Ornamentation: Surface of septa and septocostae nearly smooth, or covered with minute, irregularly shaped granulations, sparse to profuse. Granulations may coalesce to form minute, sharp, wavy, irregular ridges, visible only under the lens. Lateral ridges sometimes present; very small granulations may be set in a row along each ridge.

FOSSA: Round or oval, measuring <0·25–6·0 mm by <0·25–2·0 mm. Shallow to a few millimetres deep, depending on shape and orientation of corallites.

COLUMELLA: Weakly to well developed, sometimes absent; development variable within one corallum. Structure styliform; papillae in a row; one or a few twisted particles or plates, more or less fused; or a solid boss, often with sculptured, uneven surface. A few principal septa, to all septa, may reach columella.

NON-CALICINAL SURFACE: Almost smooth, or marked with fine, equal or subequal costae. Costae straight, slightly flexuous, or, in branching coralla, forming a fan-like pattern as do the septocostae. Number in 5 mm: 12–34. Costae smooth or with minute spines, often visible only under the lens, irregularly spaced, scattered over and between costae or set in a row along each costa. Number in 1 mm: 3–12. Underside of colonies frequently covered with encrusting organisms, such as bryozoa.

DISTRIBUTION

Indo-Pacific and Caribbean region.

BATHYMETRIC RANGE: From 3 m (GBR) to 470 m (at Hawaii, Vaughan 1907).

DISCUSSION

Of the six recent agariciid genera, *Leptoseris* seems most closely allied to *Gardineroseris* Scheer and Pillai, and especially to *Pavona* Lamarck. Indeed, the distinction between *Leptoseris* and some unifacial *Pavona* species is still somewhat uncertain. For instance, Veron and Pichon (1979) have moved *Pavona yabei* Pillai and Scheer to *Leptoseris*, though the present author considers this species a *Pavona*.

Previous descriptions of these two genera become unsatisfactory in the case of a few species whose generic position is uncertain. To labour over unequivocal genus diagnoses is not very useful when the distinction between these genera may to some extent be artificial. Since the validity of the species themselves remains unquestioned, the best course seems to be to outline the differences at species level.

Pavona yabei has close affinities with *L. mycetoseroides*. However, coralla of *P. yabei* are usually distinctive, being often much larger and forming vertically-growing vases or fluted tubes. The collines are more consistently well-developed in *P. yabei*, and the radial collines (i.e. those running from the centre to the corallum margin) are always much more prominent than in *L. mycetoseroides*. The septa and septocostae tend to be somewhat thinner and more alternating than in *L. mycetoseroides*.

Pavona cf. *explanulata* (Lamarck) *sensu* Veron and Pichon (1979) may resemble several *Leptoseris* species, notably *L. hawaiiensis*, *L. glabra*, and *L. mycetoseroides* at marginal parts which lack collines. But on the same colony, *P.* cf. *explanulata* may have thickly encrusting or massive areas as well as laminar plates, and the corallites tend to be more numerous than in *Leptoseris*. Septa and septocostae are strongly alternating, which is not the case in *L. hawaiiensis* and *L. mycetoseroides*. According to Veron and Pichon (1979), *P.* cf. *explanulata* has first order septocostae thinner than those of the second order, and septocostae which frequently branch to three or more corallites. Both these features distinguish this species from any *Leptoseris*.

L. mycetoseroides also shows some affinities with *Gardineroseris planulata* (Dana), with which it has previously been confused. Larger colonies of *G. planulata* may become very massive, and the species always lacks oval, outwardly inclined corallites which may occur near the margin in *L. mycetoseroides*. Collines are always well developed, and usually high and very acute. They frequently enclose single centres, which is much less often the case in *L. mycetoseroides*. Finally, the septa tend to be more numerous than in the *Leptoseris* species.

Leptoseris cucullata (Ellis and Solander, 1786)
(Plate 1, figs. 1–3)

Madrepora cucullata Ellis and Solander, 1786, p. 157, pl. 42.
Helioseris cucullata: Milne-Edwards and Haime, 1849, p. 72. Wells, 1973, p. 23, fig. 14.
Leptoseris nobilis: Ma, 1959, p. 17, pl. 35.

MATERIAL EXAMINED

Belize, Carrie Bow Cay, USNM 47319–22; Jamaica, DB 598, 2082, 2432; 13°11·3'N, 61°06·5'W, USNM P-878 (included with specimens of *L. cailleti*).

DESCRIPTION

CORALLUM AND CORALLITES: Corallum a thin, irregular plate, centrally attached, or encrusting with free margin. Largest colony examined measures 17·5 cm by 13 cm, several millimetres

thick, but <1 mm thick at the margin. Colour: green and brown (Colin 1978).

Corallites round or more often elliptical, measuring 1·0–6·0 mm (2·0–4·0 mm) by 1·0–6·0 mm (2·0–3·0 mm). Usually strongly inclined towards corallum margin, but sometimes sunken in. Corallites arranged singly or in rows, with up to 12 centres per row. Usually fairly crowded, but corallites or rows may be up to 1·5 cm apart. Parent sometimes distinguishable.

Where corallites are in rows, proximal cushions may form a short low ridge, 1–5 mm (2–4 mm) above the general surface, and 1–3 mm (1–2 mm) thick at the base. Ridges usually slightly inclined towards corallum margin; one specimen (USNM 47322) has short ridges and rather acute proximal cushions; these are directed upwards and give the corallum a slightly hydnophoroid appearance. Occasional raised nodular areas on some specimens, up to 8 mm high, may have corallites on them.

SEPTA: Usually strongly alternating, rarely subequal; three orders occasionally visible. Profile rounded or acute. Septal margin may be uneven but not dentate. Septa imperforate. Number per centre: 12–44 (21).

SEPTOCOSTAE: Usually strongly alternating, with first order thicker and much more exsert. Usually rather straight; rarely crenellated on raised areas. Upper margin profile acute except where septocostae well thickened. Margin non-dentate. Septocostae imperforate. Thickness: Margin (first order septocostae): <0·13–0·25 mm (<0·25 mm). Margin: (second order septocostae): to 0·13 mm (<0·13 mm). Elsewhere (first order septocostae): 0·13–0·75 mm (0·25 mm to nearly 0·5 mm). Elsewhere (second order septocostae): <0·13–0·5 mm (<0·25 mm). Number in 5 mm: Margin: 12–24 (17). Elsewhere: 11–20 (15).

SURFACE ORNAMENTATION: Septa and septocostae with small, fairly profuse granulations, though second order generally smoother. Rarely all septocostae scarcely granulated. Lateral ridges not developed.

FOSSA: Usually elliptical, measuring 0·5–2·5 mm (0·75–2·0 mm) by 0·5–1·5 mm (<1·0 mm). Fairly deep.

COLUMELLA: Absent in some specimens, in others, developed in some, but never all, fossae. A small twisted plate or knob, or a few loosely fused particles. Normally only a few (rarely most) first order septa reach the columella.

NON-CALICINAL SURFACE: Costae normally equal. Number in 5 mm: 14–22 (17). Costae smooth or with minute spines, usually set in rows on costae. Number in 1 mm: 3–7 (4).

HABITAT AND VARIATION

There is little information available on the preferred habitat of this species. Wells (1973) reports that it is not uncommon below 8 m; specimens from Carrie Bow Cay were collected on the fore-reef slope.

The small series available shows some variation in the spacing of corallites, development of short ridges, and columellar development.

DISTRIBUTION

West Indies: Belize (Carrie Bow Cay); Jamaica; St. Vincent; Barbados.

BATHYMETRIC RANGE: 6–27 m (Carrie Bow Cay) to 37–40 m (near St Vincent). Colin (1978) gives a range of from 3 m to at least 90 m.

AFFINITIES

The shape and arrangement of the corallites render this species much more similar to *Leptoseris* than to *Agaricia*. The retention of the genus *Helioseris* seems unnecessary, since a columellar structure is sometimes present.

The species is easily distinguished from other *Leptoseris*. The short ridges in some examples are quite different from the collines in *L. mycetoseroides*, from which it differs markedly in all major characters. *L. cucullata* is easily distinguished from *L. glabra*, both by its thinner septa and septocostae, and by its columellar development.

Leptoseris papyracea (Dana, 1846)
(Plate 1, fig. 4; Plate 2, figs. 1–2)

Pavonia papyracea Dana, 1846, p. 323, pl. 22, fig. 3.
Haloseris crispa: Milne-Edwards and Haime, 1851, p. 134. Rousseau, 1854, p. 120, pl. 27, fig. 2.
Pavonia pretiosa Bassett-Smith, 1890, p. 444.
Pavonia ramosa Bassett-Smith, 1890, p. 444.
Leptoseris papyracea: van der Horst, 1921, p. 30, pl. 5, fig. 7. Wells, 1954, p. 443, pl. 154, figs. 1, 2. Veron and Pichon, 1979, p. 38, figs. 65, 66.
Leptoseris digitata Vaughan, 1907, p. 140, pl. 42, figs. 1, 2. Matthai, 1924, p. 52, pl. 11, figs. 5, 7. Durham and Barnard, 1952, p. 31, pl. 2, figs. 10a, 10b. Nemenzo, 1976, p. 239, pl. 5, fig. 1.
Leptoseris panamensis Durham and Barnard, 1952, p. 36, pl. 2, figs. 11a, 11b.
Leptoseris zamboi Nemenzo, 1971, p. 158, pl. 5, figs. 4, 5.

Material Examined

NON-GBR MATERIAL: Amirante Is., BM E.16; Macclesfield Bank, BM 1892.10.17.130 (*Pavonia ramosa* holotype); Tizard Bank, BM 16B (*Pavonia pretiosa* holotype); Philippines, PM 119 (mentioned Milne-Edwards and Haime, 1851, as *Haloseris crispa*); Hawaii, USNM 20892 (*Leptoseris digitata* cotype); Panama, AHF 1 (*Leptoseris panamensis* holotype); Colombia, AHF 10·4 (mentioned Durham and Barnard, 1952, as *Leptoseris digitata*); Coco I., AHF 10·3 (mentioned Durham and Barnard, 1952, as *Leptoseris digitata*); Ecuador, AHF 11·2 (*Leptoseris panamensis* paratype).

GBR MATERIAL: Townsville Region: Between 18°50'S–19°01'S and 146°58'E–147°07'E, BM 1979.4.1.1, USNM 54210, QM G12248–9, ZD 20292, 20294–5.

Description

CORALLUM AND CORALLITES: Corallum small and delicate, of twisted branches which tend to widen towards the tip. Largest colony collected measures 5 cm by 4·5 cm, up to 4 mm thick at the base but <1 mm at the margin. Nemenzo (1971) described a larger colony. Colour: pale brown.

Corallites round or elliptical, measuring approximately 1·0–3·5 mm (2·0–3·0 mm) across. There is usually space for one corallite only within the branch width, but occasionally there are two abreast. Corallites superficial, slightly sunken or sometimes slightly inclined towards branch tips. Corallites usually a few millimetres apart along branches, but up to >1 cm.

SEPTA: Equal or subequal, sometimes a few markedly thicker and more exsert than the rest. Profile usually rounded. Margin sometimes uneven, but not dentate; septa imperforate. Number per centre: 8–22 (14).

SEPTOCOSTAE: Equal or subequal, tending to diverge as branches widen and new septocostae are inserted. A few septocostae may be especially thickened and exsert. Upper margin profile rounded, acute, or slightly flattened. Margin may be ragged but rarely dentate. Dentations present on a few specimens (e.g. the types of *P. ramosa*, BM 1892.10.17.130, and *L. digitata*, USNM 20892), these minute, irregularly spaced, 5–10 in 1 mm. Septocostate usually imperforate. Thickness: Margin: <0·13–0·25 mm (<0·25 mm). Elsewhere: <0·13–0·75 mm (0·25 mm). Number in 5 mm: (very variable according to pattern of insertion of septocostae) Margin: 16–28 (20). Elsewhere: 12–20 (16).

SURFACE ORNAMENTATION: Septa and septocostae rather well granulated; granulations may occur as sharp, wavy ridges. Lateral ridges sometimes present, usually not well developed.

FOSSA: Round or elliptical, measuring 0·25–2·0 mm (<1·0 mm) across. Rather shallow.

COLUMELLA: Variably developed, sometimes absent, especially in young corallites. A small pillar; a few twisted particles or plates; or a solid boss. Few to the majority of septa reach the columella.

NON-CALICINAL SURFACE: Marked with fine costae. Number in 5 mm: 16–30 (22). Costal spines in rows or scattered. Number in 1 mm: 4–12 (7). Costae sometimes reduced to rows of spines, and direction of costae may then be unclear.

Habitat and Variation

Material has been collected from soft-bottom biotopes of coarse sand and mud, at stations over 25 km offshore, in deeper water. Unlike *L. gardineri*, it has not been found in the close vicinity of fringing reefs, and apparently occupies a different type of biotope.

Although there is some variation in branch shape, septal number, presence of minute dentations on the septocostae, and columellar development, the series of specimens (from a wide geographical range) is very consistent.

Distribution

Indo-Pacific: Madagascar; Amirante Is.; Andaman Is.; South China Sea; Indonesia; Sulu Sea; Philippines; Great Barrier Reef; Marshall Is.; Hawaii; Panama; Colombia; Coco I.; Ecuador.

BATHYMETRIC RANGE: 26–35 m (GBR); 108–176 m (at Bikini, Wells 1954).

Affinities

This species is easily distinguished from *L. gardineri* by its much smaller, thinner branches and superficial corallites. In growth form it resembles its West Indian counterpart, *L. cailleti*, but the latter has much better circumscribed corallites which are strongly inclined towards branch tips.

Leptoseris cailleti (Duchassaing and Michelotti, 1864)
(Plate 2, figs. 3–4)

Mycedium cailleti Duchassaing and Michelotti, 1864, p. 93 (reprint). Pourtalès, 1874, p. 44, pl. 9, figs. 1, 2.
Agaricia cailleti: Vaughan, 1901, p. 311, pl. 20.

MATERIAL EXAMINED

20°00·4'N, 71°40·7'W, USNM P–1148; 12°15·4'N, 69°57·5'W, USNM P–760; Off Mayagüez, Puerto Rico, USNM 54215, 54216; Off St Thomas, USNM 6079; 15°33·7'N, 61°14·7'W, USNM P–932; 13°11·3'N, 61°06·5'W, USNM P–878.

DESCRIPTION

CORALLUM AND CORALLITES: Corallum of delicate, twisted branches which widen from the base; branches may fuse, or occasionally curl to form tubes. Branches measure <5 mm thick at base, often <1 mm thick at margin; and 0·5–3·0 cm (<1·0–2·0 cm) across. Sometimes dead at the base. Largest colony measures 8 cm high and 12 cm wide. Colour: light brown.

Corallites round or more often elliptical, measuring 1·0–4·0 mm (1·5–2·5 mm) by 1·0–4·0 mm (1·0–<2·0 mm). Sometimes flush or slightly sunken, but usually strongly inclined towards branch tips. Usually scattered, occasionally in rows with up to six centres per row. Often close; rarely up to 8 mm apart along branches. Proximal cushions low, 0·5–1·0 mm above the general surface.

SEPTA: Equal, sometimes subequal, profile normally rounded. Septa non-dentate, imperforate. Number per centre: 6–26 (16).

SEPTOCOSTAE: Equal, occasionally subequal with first order slightly more exsert. Straight or slightly flexuous, with upper margin profile usually acute. Septocostae non-dentate, imperforate. Thickness: Margin: <0·13–0·25 mm (<0·25 mm). Elsewhere: 0·13–0·38 mm (0·25 mm). Number in 5 mm: Margin: 18–30 (21). Elsewhere: 16–26 (19).

SURFACE ORNAMENTATION: Sides of septa and septocostae with small, fairly profuse granulations. Lateral ridges not developed.

FOSSA: Usually elliptical, measuring <0·5–2·0 mm (<1·0 mm) by <0·25–1·0 mm (0·25–0·5 mm). Shallow to fairly deep.

COLUMELLA: Poorly to well developed. Of a few twisted particles, more or less fused, sometimes in a row; or a more solid boss with sculptured surface. Few to most septa may reach columella; in general, about half the septa reach.

NON-CALICINAL SURFACE: Marked with fine but distinct costae, equal or a few particularly thickened. Number in 5 mm: 20–30 (22). Costal spines usually present, in a row along each costa; spines often more conspicuous than in other *Leptoseris* species. Number in 1 mm: 4–9 (6).

HABITAT AND VARIATION

The series available is small but represents a variety of localities. All specimens are remarkably similar, and the only notable variation is in branch shape and columellar development.

Few collections have been made of this apparently rare species, which has been found in comparatively deeper water. Puerto Rican specimens (USNM 54215 and 54216) were collected at 48 m on a sponge bank about 6 km long, 16 km off the coast. This area is exposed to strong currents (1 knot or more), and exposed to strong swell which comes through the Mona channel during the winter, and which runs in a direction opposite to the current. Even at this depth, there can be some effects of swell (P. Colin, pers. comm.). Specimens were in small depressions or alongside other objects such as large sponges.

DISTRIBUTION

Caribbean region: Approximately 9°–20°N, 61°–78°W. This includes the Antilles from the Dominican Republic to Barbados; Curaçao; and the north coast of Panama.

BATHYMETRIC RANGE: 33–40 m (near Dominica) to 60–68 m (near Curaçao). Pourtalès (1874) reports a dead specimen from 183 m at Barbados.

AFFINITIES

The growth form of *L. cailleti,* and the structure and arrangement of the corallites, suggest it is much more closely allied to *Leptoseris* than to *Agaricia.* In some respects it may, ecologically speaking, be the Atlantic counterpart of *L. papyracea.* The species are easily distinguished by the quite different nature of the corallites.

Leptoseris incrustans (Quelch, 1886)
(Plate 3, figs. 1–2)

Cylloseris incrustans Quelch, 1886, p. 124, pl. 6, figs. 4–4b.
Leptoseris incrustans: Ma, 1959, *(pars)*, p. 17, pl. 31.
not *Leptoseris incrustans* Gardiner, 1905, p. 948, pl. 92, fig. 25 (= *L. hawaiiensis* Vaughan).

MATERIAL EXAMINED

Tahiti, BM 1886.12.9.171–2 *(Cylloseris incrustans* cotypes).

DESCRIPTION

CORALLUM AND CORALLITES: Corallum partly encrusting with free margin, reflected downwards. Both specimens entire, growing over dead pieces of the same species. Larger specimen measures 8·5 cm by 5 cm; thickness at margin <1 mm; elsewhere 2–3 mm between projections, up to 10 mm thick including projections.

Corallites round or elliptical, measuring 1·0–3·5 mm (1·0–2·0 mm) by 1·0–1·5 mm (1·0 mm). Close, numerous, often superficial and flush or slightly sunken in. Corallites often in no particular orientation, but near the edge they may be inclined towards corallum margin. Occasionally in short rows, with up to eight centres per row, usually less. Corallites up to 6 mm apart, generally less; parent not distinguishable.

Corallum has numerous, rather pointed, hydnophoroid projections, raised 2–4 mm (2–3 mm) above the general surface. Projections often with elongate rather than round base. Length at base is 2–7 mm, width at base 1–2 mm. Often arranged in no particular relation to corallites. Proximal cushions may be slightly pointed and resemble projections.

SEPTA: Equal, thin, often well spaced. Profile usually acute. Non-dentate, imperforate. Number per centre: 12–27 (14–20).

SEPTOCOSTAE: Equal, often flexuous due to projections and close corallites; sometimes contorted over raised areas. Upper margin profile usually acute. Non-dentate, imperforate. Thickness: Margin: <0·13–0·25 mm (~0·13 mm). Elsewhere: 0·13–0·25 mm (slightly under 0·25 mm). Number in 5 mm: Margin: 28–32 (30). Elsewhere: 21–28 (23).

SURFACE ORNAMENTATION: Sides of septa and septocostae with very small, profuse granulations. Lateral ridges present, rather weakly developed.

FOSSA: Usually elliptical, measuring 0·75–1·25 mm (1·0 mm) by 0·5–0·75 mm. Shallow.

COLUMELLA: A style or small knob, round or compressed. Most septa meet the columella, though sometimes only near the base of styliform columellae.

NON-CALICINAL SURFACE: Costae low, equal. Number in 5 mm: 22–30. Costal spines, where present, usually scattered rather than in rows. Number in 1 mm: 6–8.

HABITAT AND VARIATION

Quelch gives no habitat information for this species. Since only two, very similar specimens are available, it is not possible to comment on the variation. It should be noted that the specimens were collected in a marginal region, in terms of coral diversity and reef development.

DISTRIBUTION

Indo-Pacific: Tahiti.

BATHYMETRIC RANGE: Not known.

AFFINITIES

This species has previously been confused with *L. hawaiiensis* (including its synonym *L. incrustans* Gardiner) and with *L. mycetoseroides*. A further, unregistered specimen from Hawaii, which seems to belong in *L. incrustans,* suggests that the species has close affinities with *L. hawaiiensis*. However, *L. incrustans* does appear to be a valid species, distinguished from *L. hawaiiensis* by its numerous hydnophoroid projections and small, often superficial corallites.

Leptoseris solida (Quelch, 1886)
(Plate 3, fig. 3; Plate 4, figs. 1–3)

Domoseris solida Quelch, 1886, p. 126, pl. 5, figs 5, 5a.
Domoseris porosa Quelch, 1886, p. 125, pl. 5, figs. 4–4c.
Leptoseris solida: Wells, 1954, p. 444, pl. 154, figs. 8, 9.
Leptoseris paschalensis Wells, 1972, p. 186, fig. 1, *4*, fig. 2, *1–3*, *ig. 3, 1–3*.

MATERIAL EXAMINED

Bikini Atoll, USNM 44799 (mentioned Wells, 1954); Tahiti, BM 1886.12.9.177 (*Domoseris solida* holotype), 1886.12.9.296 (*Domoseris porosa* holotype); Easter I.,

USNM 53156 (piece of holotype of *Leptoseris paschalensis*), MHD76 (piece of paratype of *Leptoseris paschalensis*).

Description

CORALLUM AND CORALLITES: Corallum plate-shaped or encrusting. Largest colony measures 25 cm by 22 cm, about 1 cm thick centrally, <1 mm thick at the margin.

Corallites round or elliptical, measuring 1·0–5·0 mm (2·0–4·0 mm) by 1·0–4·0 mm (2·0–3·0 mm). Corallites sometimes sunken in, but usually strongly inclined towards corallum margin. Scattered or sometimes in short rows, with up to six centres per row. Corallites very close or up to 2 cm apart.

Proximal cushions up to 5 mm high. Corallum often has rounded nodules, similar in shape to proximal cushions, up to 5 mm high, arranged in no particular relation to corallites.

SEPTA: Unequal in size, sometimes clearly alternating, sometimes with a few septa especially thickened and exsert. Profile usually rounded. Septa non-dentate, occasionally perforate. Number per centre: 8–26 (15).

SEPTOCOSTAE: Usually strongly alternating, with some septocostae particularly thick and exsert; more equal near corallum margin. Often very contorted and crenellated over proximal cushions and nodules; even here, first order septocostae remain more exsert. Upper margin profile usually rounded, but in second order septocostae it may be acute, or flattened with a narrow ridge down the centre. Margin not dentate, but often uneven in that it forms long, wave-like undulations; these are low, extending 0·5–2·5 mm (>1·0 mm) along the septocostal margin. This gives septocostae an irregular appearance; however, margin is never divided into the distinct, peg-like teeth typical of *L. scabra*.

Septocostae sometimes perforate. Thickness: Margin (both orders): <0·13–0·38 mm (0·25 mm or less). Elsewhere (first order septocostae): <0·13–1·0 mm (0·25–0·5 mm). Elsewhere (second order septocostae): <0·13–0·5 mm (<0·25–0·38 mm). Number in 5 mm: Margin: 15–23 (19). Elsewhere: 14–20 (16).

SURFACE ORNAMENTATION: Septa and septocostae, especially those of the first order, well granulated; granulations rough, rather profuse, sometimes coalescing to form sharp, wavy ridges. Lateral ridges sometimes developed, mostly on second order septocostae.

FOSSA: Round or elliptical, measuring <0·25–2·0 mm (0·5–1·0 mm) by <0·25–0·5 mm. Usually deep.

COLUMELLA: Weakly to well developed. Usually of twisted particles, more or less fused; occasionally a boss. Few to many septa, but usually at least half, reach the columella.

NON-CALICINAL SURFACE: Costae equal or subequal. Number in 5 mm: 14–23 (19). Smooth, or covered with small spines, scattered or in a row along each costa. Number in 1 mm: 6–10 (7). In his description of *L. paschalensis*, Wells (1972) reports juvenile, mono- to tricentric offsets on the non-calicinal surface.

Habitat and Variation

There is little information regarding the habitat of this species. The series available is small, but shows some variation in growth form, arrangement of corallites and thickness of septa and septocostae. In particular, Wells' holotype of *L. paschalensis* (USNM 53156) has thinner septocostae with a more even margin.

Distribution

Indo-Pacific: Marshall Is.; Tahiti; Easter I.

BATHYMETRIC RANGE: 40–100 m (at Easter I., Wells 1972) to 106–165 m (at Bikini, Wells 1954).

Affinities

This species has previously been confused with *L. scabra*. However, the septocostae in *L. solida* may have an undulating margin, but this is never divided into the distinct teeth found in *L. scabra*. Furthermore, *L. solida* has smaller corallites with fewer septa and smaller fossae, and corallites are usually more strongly inclined towards the corallum margin.

L. solida has some affinity with *L. glabra* in that the septocostae are fairly thick, strongly alternating and basically non-dentate. However, the latter species is easily distinguished by its larger corallites with more septa, better developed columella, and much straighter septocostae.

Leptoseris hawaiiensis Vaughan, 1907
(Plate 4, fig. 4; Plates 5–7)

Leptoseris striatus Saville-Kent, 1871, p. 284. (*Nomen oblitum*)

Leptoseris hawaiiensis Vaughan, 1907, p. 137, pl. 39, pl. 40. Matthai, 1948, p. 192, pl. 4, figs. 9, 10. Wells, 1954, p. 444, pl. 154, figs. 3, 4. Veron and Pichon, 1979, p. 52, figs. 92–8, 740.

Leptoseris tubulifera Vaughan, 1907, p. 141, pl. 42, fig. 3, pl. 43.

Leptoseris gravieri van der Horst, 1922, p. 422.

Leptoseris incrustans Gardiner, 1905, p. 948, pl. 92, fig. 25.

Leptoseris incrustans (Quelch): Wells, 1954, p. 444, pl. 154, figs. 5–7.

not *Cylloseris incrustans* Quelch, 1886, p. 124, pl. 6, figs. 4–4b.

not *Leptoseris tubulifera:* van der Horst, 1921, p. 30, pl. 5, fig. 8. (= juvenile ? *L. scabra*, ? *L. glabra*).

MATERIAL EXAMINED

NON-GBR MATERIAL: Amirante Is., BM 1937.11.17.123 (*Leptoseris gravieri* holotype); Reunion, GF REU.254, REU.812, REU.831–2, REU.899; Chagos Is., TWCMS C9055, C9058–9, C9061, C9063, C9066, C9074, C9080, C12403, C12408; Maldives, CM Registered but not numbered. (*Leptoseris incrustans* Gardiner holotype); Borneo, BM 1851.1.20–12 (*Leptoseris striatus* holotype); Paternoster Is., AM Coel 695 (incorrectly labelled type of *Leptoseris tenuis*); Philippines, MP 1811–75, 2656–75; Bikini Atoll, USNM 44796, 44798 (mentioned Wells, 1954, as *Leptoseris incrustans*); Eniewetak, EN 2869; Hawaii, USNM 20843–5, 20875–6 (*Leptoseris hawaiiensis* cotypes); USNM, 20846 (*Leptoseris tubulifera* cotype); Tahiti, ZD 20325.

GBR MATERIAL: Lizard I. region: Jewell Reef — Outer Slope, QM G12254, G12269, G12274, G12282, ZD 9193, 9205, 9232, 9256, 20284. Carter Reef — Outer Slope, ZD 9840; Knoll, back reef, BM 1979. 4.2.3, ZD 9600; Channel to N. of Carter Reef; BM 1979.4.2.8, 1979.4.2.12, QM G12284, ZD 9768–9, 20302. Yonge Reef — Outer slope, QM G12255, G12261, G12268, MP 2636, 2638, ZD 9789, 9792, 9798, 10571–4, 10872, 20169; Back reef, BM 1979.4.2.5, USNM 54203, QM G12250, G12257, G12262–3, G12278, ZD 9570, 9573, 9779–81, 9783, 10579, 10656, 10680; Channel to N. of Yonge Reef, BM 1979.4.2.4, ZD 9761, 10920, 20303. Unnamed reef S. of Yonge Reef — Channel to N. of reef, BM 1979.4.2.2. S. Ribbon Reef — Back reef, BM 1979.4.2.10–11, USNM 54202, QM G12252–3, G12265, G12267, G12272, G12275, G12283, ZD 20260; Plug Reef, S. end of reef, QM G12271, G12273. Lizard I. — Area 2, ZD 20067, 20086; Area 3, BM 1979.4.2.9, USNM 54204, QM G12251, G12258, G12258–60, G12264, G12266, G12276, G12279, G12281, ZD 20043; Area 4, ZD 9814

Palm Is. Group: Pelorus Is., W. side, BM 1979.4.2.1, 1979.4.2.7. Eclipse Is., QM G12256.

Townsville region: Keeper Reef, SE. side, ZD 20246. Heron I. Region: Heron Reef, N. side, BM 1979.4.2.6, QM G12270, G12277, G12280, ZD 10699.

DESCRIPTION

CORALLUM AND CORALLITES: Corallum commonly encrusting with free margin; sometimes plate or bowl-shaped, or entirely encrusting; rarely tubuliferous or foliose. Largest colony collected measures 39 cm by 34 cm, >1 cm thick but <1 mm at the margin. Some plate-shaped and encrusting coralla may be extremely thin. Colour: Dark to light brown or beige, rarely green or dark red. Sometimes patchy, e.g. brown with green, red, or beige patches. Occasionally a white margin.

Corallites round or oval, measuring 1·0–7·0 mm (2·0–5·0 mm) by 1·0–5·0 mm (2·0–4·0 mm). Often flush or slightly sunken; sometimes with raised rims and directed upwards; or inclined towards corallum margin. Corallites sparse or crowded; scatered or in short rows, with up to 12 centres per row. Corallites or rows up to >3 cm apart. Parent corallite sometimes distinguishable.

Corallum occasionally with nodules, up to 5 mm high. Tubes, when present, up to 8 mm wide, usually less. Proximal cushions up to 5 mm high.

SEPTA: Equal or subequal, profile rounded or acute. Margin non-dentate, though sometimes uneven. Septa rarely perforate. Number per centre: 8–48 (21).

SEPTOCOSTAE: Equal or subequal; usually straight or slightly flexuous, but sometimes very contorted over raised areas, especially on encrusting coralla. Upper margin profile often very acute and pointed rather than tapering. Margin non-dentate, or with minute dentations, 3–10 (7) in 1 mm. On some specimens margin is slightly pitted and discontinuous; this condition is often associated with perforate septocostae. However, septocostae most often imperforate. Thickness: Margin: <0·13–0·38 mm (<0·25 mm). Elsewhere: 0·13–0·38 mm (0·25–0·38 mm). Number in 5 mm: Margin: 20–30 (23). Elsewhere: 15–26 (19).

SURFACE ORNAMENTATION: Septa and septocostae lightly and minutely granulated. Lateral ridges often well developed.

FOSSA: Usually elliptical, measuring 0·25–5·0 mm (0·5–1·0 mm) by <0·25–0·75 mm (0·5 mm). Shallow to rather deep.

COLUMELLA: Weakly to fairly well developed. Generally rather a loose structure of twisted particles; sometimes a solid boss. The number of septa reaching the columella varies from few to all septa, though often shorter septa do not reach columella.

NON-CALICINAL SURFACE: Costae equal or subequal. Number in 5 mm: 16–27 (22). Costal spines scattered or in rows on costae. Number in 1 mm: 4–9 (6).

HABITAT AND VARIATION

This species is most frequently found on Outer Barrier reefs, where it is not uncommon in overhangs and caves (especially on the ceilings and back walls). It has a definite preference for a shaded environment; and rarely occurs in very turbid water conditions.

There is considerable variation in growth form and corallite size and arrangement. For example, some specimens (including Vaughan's cotype USNM 20843) are very thin with small, sparse corallites directed upwards. Heavier coralla (thick plates and thick encrusting colonies) tend to have larger, more numerous corallites, slightly sunken, or directed towards corallum margin, and sometimes contorted septocostae. A few specimens (e.g. ZD 9570) exhibit a variety of corallite types within one corallum. These differences are not readily related to differences in micro-habitat. However, Australian specimens resembling Vaughan's cotype (USNM 20843) have been collected in very poorly illuminated conditions. Thinly encrusting colonies with numerous, rather superficial corallites have been found most often on the ceilings of caves.

DISTRIBUTION

Indo-Pacific: Red Sea; Amirante Is.; Reunion; Chagos Archipelago; Maldive Is.; Thailand; Borneo; Seringapatam Atoll (NW. Australia); Indonesia; Philippines; Great Barrier Reef; Marshall Is.; Hawaii; Tahiti.

BATHYMETRIC RANGE: 3–46 m (GBR); 470 m (at Hawaii, Vaughan 1907).

AFFINITIES

This species is mostly closely allied to *L. mycetoseroides*. In particular, specimens with close but poorly delineated corallites may resemble *L. mycetoseroides* in which collines are absent or very poorly developed. In such cases, *L. hawaiiensis* is best distinguished by its septocostae, which are often fewer and less granulated, with a more pointed upper margin profile, and better developed lateral ridges.

Leptoseris scabra Vaughan, 1907
(Plates 8–9)

Domoseris regularis Quelch, 1886, p. 127, pl. 5, figs. 6–6b. *(Nomen oblitum).*

Leptoseris scabra Vaughan, 1907, p. 139, pl. 41, figs. 1, 1a, 2. Wells, 1954, p. 444, pl. 155, figs. 1, 2. Veron and Pichon, 1979, p. 48, figs. 83–91, 739.

Leptoseris columna Yabe and Sugiyama, 1941, p. 75, pl. 63, figs. 2–2d.

Leptoseris explanata Yabe and Sugiyama, 1941, p. 75, pl. 63, figs. 3–3e.

MATERIAL EXAMINED

NON-GBR MATERIAL: Reunion, GF REU.835, REU.849, REU.853, REU.893, REU.897, REU.901; Mauritius, GF MAU-849; Chagos Is., TWCMS C9070–3, C9076–8, C9086–8, C9090–1, C9097, C9099–100; Palau, UT 64333 (*Leptoseris columna* holotype), 64334 (*Leptoseris explanata* holotype); Bikini Atoll, USNM 44801 (mentioned Wells, 1954); Hawaii, USNM 20886 (*Leptoseris scabra* cotype); Tahiti, BM 1886.12.9.295 (*Domoseris regularis* cotype).

GBR MATERIAL: Lizard I. region: Jewell Reef—Outer slope, BM 1979.4.3.1, 1979.4.3.4, QM G12290, G12330, ZD 9192–3, 20312–13. Carter Reef—Knoll, back reef, USNM 54212, QM G12324, ZD 9613; Channel to N. of Carter Reef, BM 1979.4.3.10, USNM 54211, ZD 9765. Yonge Reef—Outer slope, MP 2637, 3492, 3759, ZD 9748, 9791, 9819; Back reef, ZD 10578; Channel to N. of Yonge Reef, BM 1979.4.3.11, QM G12288, ZD 9744, 9746, 9750–1. Unnamed reef S. of Yonge Reef—Channel to N. of reef, QM G12295, ZD 10348. S. Ribbon Reef—Back reef, QM G12321. Lizard I.—Area 1, QM G12319, G12327, G12331, ZD 9940, 10032–3; Area 2, BM 1979.4.3.14, USNM 54214, QM G12289, G12291, G12294, G12303, G12305, G12307, G12320, G12326, G12332–3, ZD 9037, 9125, 9273, 9577, 9579, 9581–2, 9586, 9631, 9776, 9910, 10127, 10215, 10974; Area 3, BM 1979.4.3.15, QM G12297, G12299, G12302, G12323, G12325, MP 2737, ZD 9270, 9273, 9275, 9335, 9338, 9340, 9342, 9802, 10236, 10241, 10301, 10342–3, 10349, 10354–5, 10364, 10597, 20315, 20317; Area 4, BM 1979.4.3.8, QM G12292, G12301, G12308, G12322, G12328, MP 3244, ZD 9371, 9382–4, 9833, 10175, 10178, 10622, 20128, 20314, 20318–21. Nymph I., QM G12298, G12334, ZD 9285, 9292. MacGillivray Reef, QM G12316. North Direction I., ZD 10552.

Palm Is. Group: Pelorus I., W. side, BM 1979.4.3.5, 1979.4.3.7, QM G12287, G12296, G12304, G12306, G12309, G12313, ZD 9524. Orpheus I., Pioneer B., BM 1979.4.3.13, QM G12285, G12314, ZD 9520, 9528, 9878, 9909. S. Calliope Channel; BM 1979.4.3.2; QM G12293, ZD 9526. Curacoa I., SW. side; BM 1979.4.3.6, 1979.4.3.12, QM G12317, ZD 20322. Great Palm I., NW. side, BM 1979.4.3.3, 1979.4.3.9, QM G12300, G12311–12, ZD 9838. Eclipse I., USNM 54213, QM G12286, G12315, G12318, G12329. Brisk I., QM G12310, ZD 20323.

DESCRIPTION

CORALLUM AND CORALLITES: Corallum usually encrusting with free margin; sometimes plate- or bowl-shaped, or erect with a foliose margin which may curl around to form low tubes. The largest colony collected measures 33 cm by 30 cm, and up to >1 cm thick, but less at the margin. Colour: Usually mid-brown, sometimes green, browny-green, or beige; rarely mauve or grey. Occasionally a combination of colours, e.g. pale nodules or darker septocostae. Sometimes a white margin.

Corallites usually elliptical, measuring 2·0–10·0 mm (3·0–6·0 mm) by 2·0–7·0 mm (2·0–4·0 mm). Corallites sometimes flush or slightly sunken, but usually with raised rims and directed upwards or towards corallum margin. Sparse or crowded; scattered, or arranged in roughly concentric rows (especially in flatter colonies or near the margin). Up to 20 centres per row, but often <10. Corallites or rows up to >3 cm apart; parent corallite sometimes distinguishable.

Proximal cushions up to 5 mm high. Nodules, not necessarily adjacent to corallites, up to 8 mm high.

SEPTA: Generally strongly alternating, with first order much thicker and more exsert; sometimes one or two septa particularly thickened. Septa rarely equal. Profiile usually rounded. Margin may be uneven but not dentate; septa usually imperforate. Number per centre: 10–48 (24).

SEPTOCOSTAE: Rarely equal, usually strongly alternating even at the margin. Sometimes fairly straight between centres, but often very labyrinthine over proximal cushions and nodules. Here second order septocostae may become as thickened as those of first order. Upper margin profile of first order septocostae rounded or subacute; second order septocostae usually with flatter margin with a narrow ridge down the centre. First order septocostae dentate, bearing irregular, often blunt, peg-like dentations. Height from crest to base is 0·13–0·75 mm (0·25–0·5 mm). Spacing 6–18 (10) in 5 mm. Second order septocostae sometimes with similar though smaller dentations, but frequently non-dentate. Dentations often best developed on proximal sides of corallites. Occasionally, if septocostae equal, all septocostae may have smaller, more regular dentations along entire length of margin between centres.

Septocostae perforate or imperforate. Thickness: Margin (first order septocostae): 0·13–0·5 mm (0·25–0·38 mm). Margin (second order septocostae): <0·13–0·38 mm (0·25 mm or less). Elsewhere (first order septocostae): 0·25–0·75 mm (0·38–0·5 mm). Elsewhere (second order septocostae): 0·13–0·5 mm (0·38 mm). Number in 5 mm: Margin: 15–28 (21). Elsewhere: 11–24 (17).

SURFACE ORNAMENTATION: Sides of septa and septocostae, especially those of first order, well granulated; granulations rough, sometimes coalescing to form sharp, wavy ridges. Lateral ridges conspicuous on thinner, second order septocostae.

FOSSA: Usually elliptical, measuring 0·5–4·0 mm (1·0–2·0 mm) by 0·25–1·0 mm (0·25–0·75 mm). Often deep.

COLUMELLA: Weakly to well developed. Structure a style; a few twisted particles, more or less fused; a solid boss; or papillae in a row in very elliptical fossae. Number of septa reaching columella varies from a few septa, to most septa if columella well developed. In general, most first order septa reach columella, most second order septa do not.

NON-CALICINAL SURFACE: Costae equal or subequal. Number in 5 mm: 16–26 (21). Spines, where present, often scattered over costate. Number in 1 mm: 4–12 (8).

HABITAT AND VARIATION

L. scabra is one of the commonest species of *Leptoseris*. It occurs unshaded on soft bottoms or firm substrates, also in crevices, overhangs and caves (most frequently on the back or side walls). Colonies from areas with high sedimentation rates tend to be more erect, with curled or foliose margins. Larger, plate-shaped colonies have been collected mostly in clearer water, from exposed stations at Lizard I. and at the Outer Barrier. More encrusting colonies are common in a variety of biotopes.

Most specimens are typically very scabrous. However, some specimens (representing a variety of growth forms) have areas of the corallum in which the septocostae are much smoother and less alternating; a few specimens are scarcely dentate throughout. This variation does not seem to be related to habitat differences. Specimens with equal and often more regularly dentate septocostae were collected at Outer Barrier stations,

alongside specimens with more typically alternating and dentate septocostae, and this difference may well be genetic.

DISTRIBUTION

Indo-Pacific: Reunion; Mauritius; Chagos Archipelago; Houtman Abrolhos Is.; Palau; Great Barrier Reef; Solomon Is.; Marshall Is.; Hawaii; Tahiti.

BATHYMETRIC RANGE: 5–55 m (GBR); 143–406 m (at Hawaii, Vaughan 1907).

AFFINITIES:

Unusual examples of this species with less alternating, less scabrous septocostae may come close to specimens of *L. glabra* with less alternating septocostae. *L. scabra* is also closely related to *L. solida*, as discussed previously.

Leptoseris gardineri van der Horst, 1921 (Plate 10)

Leptoseris gardineri van der Horst, 1921, p. 30. Hoffmeister, 1925, p. 41, pl. 4, fig. 2. Yabe and Sugiyama, 1941, p. 73, pl. 63, figs. 1–1c. Wells, 1954, p. 444. Veron and Pichon, 1979, p. 40, figs. 67–70.

Folioseris papyracea: Rehberg, 1892, p. 26, pl. 2, fig. 8, pl. 4, fig. 2.

Leptoseris papyracea: Gardiner, 1905, p. 947, pl. 92, fig. 23.

MATERIAL EXAMINED

NON-GBR MATERIAL: Indonesia, Lombok, AM Siboga-Expeditie, Stat. 19.

GBR MATERIAL: Palm Is. Group: Pelorus I., W. side, BM 1979.4.4.1., 1979.4.4.4, ZD 9538. Orpheus I., Pioneer B., BM 1979.4.4.2, QM G12335–7, G12339, ZD 9532, 9534, 9540, 9891–5, 9897–8, 9902–4. Great Palm I., Butler B., QM G12338. Eclipse I., BM 1979.4.4.3, USNM 54201. Esk I., ZD 9536.

DESCRIPTION

CORALLUM AND CORALLITES: Corallum erect and branching, branches often >20 cm high, 1–3 cm wide; branches may fuse. Branches fairly flat, or somewhat curled with calicinal surface innermost. Margin may be reflected onto non-calicinal surface for >1 cm, and corallites may develop here so that at the margin, corallum appears bifacial. Bases of branches, buried in sediment, frequently dead. Colonies may consist of a few branches, or stands several metres across. Colour: Brown or beige, sometimes with a white margin.

Corallites round or elliptical, measuring 2·0–8·0 mm (4·0–6·0 mm) by 2·0–6·0 mm (3·0–4·0 mm). Often with raised rims, directed upwards or towards branch ends; sometimes flush. Scattered or up to three abreast on a branch; close or >3 cm apart along branches.

SEPTA: Subequal to alternating, with first order septocostae thicker and more exsert. Profile usually rounded, sometimes acute. Septa non-dentate, imperforate. Number per centre: 10–36 (24).

SEPTOCOSTAE: Alternating, with first order septocostae especially thicker; less alternating at margin. As branches widen, second order septocostae become first order ones. Upper margin profile of first order septocostae rounded; second order septocostae with rounded profile, or margin may be flat with a narrow ridge down the centre. Septocostae non-dentate, imperforate. Thickness: Margin: 0·13–0·5 mm (0·25 mm). Elsewhere: 0·13–0·75 mm (0·25–0·38 mm). Number in 5 mm: Margin: 14–24 (18). Elsewhere: 12–18 (15).

SURFACE ORNAMENTATION: Surface of septa and septocostae, especially those of first order, well granulated, sometimes with sharp, wavy ridges. Lateral ridges more conspicuous on thinner, second order septocostae.

FOSSA: Usually elliptical, measuring 0·5–2·5 mm (1·0–2·0 mm) by <0·5–2·0 mm (0·5–1·0 mm). Shallow to fairly deep.

COLUMELLA: Poorly to well developed. A few twisted particles, or a more solid boss. All septa may reach columella, but usually only those of the first order.

NON-CALICINAL SURFACE: Often distinctly costate, with costae tending to diverge and become more numerous towards branch tips. Number in 5 mm: 12–22 (18). Costal spines minute, scattered or in rows along costae. Number in 1 mm: 4–8 (6).

HABITAT AND VARIATION

This species occurs on soft bottoms, often in conditions of high sedimentation and turbid water, and specimens were collected in relatively shallow water in the vicinity of fringing reefs. There may be considerable variation in branch shape and size, even within one colony. However, most skeletal characters are rather consistent, despite some variation in corallite size, and the extent to which septa and septocostae are alternating.

Distribution

Indo-Pacific: Maldives; Indonesia; Palau; Great Barrier Reef; Marshall Is.; Samoa.

Bathymetric Range: 10–18 m (GBR); to 55 m (at Bikini, Wells 1954).

Affinities

This species is most closely allied to *L. glabra*. However, coralla of *L. glabra*, if branching, have wider branches; the corallites are larger with more septa per centre, and septa and septocostae are generally more alternating than in *L. gardineri*.

Leptoseris mycetoseroides Wells, 1954
(Plates 11–13)

Leptoseris? mycetoseroides Wells, 1954, p. 445, pl. 153, figs. 4–6.
Leptoseris incrustans: van der Horst, 1922, p. 422, pl. 32, figs. 3, 4. Ma, 1959 (*pars*), p. 17, pl. 30, pl. 32, figs. 3, 4.
Agaricia (?) *minikoiensis:* Yabe, Sugiyama, and Eguchi, 1936, p. 55, pl. 42, figs. 5–7.
Agaricia (Agariciella) minikoiensis: Ma, 1937, p. 149, pl. 45, figs. 2, 3.
Leptoseris mycetoseroides: Veron and Pichon, 1979, p. 57, figs. 99–103, 741.
not *Agaricia ponderosa* var. *minikoiensis* Gardiner, 1905, p. 937, pl. 90, fig. 7.

Material Examined

Non-GBR Material: Madagascar, MPIO 127–67, 142–67, 534–67, 539–67, 1131–69; Reunion, GF REU.96, REU.217, REU.320, REU.386, REU.518, REU.872; Mauritius, GF MAU.355. MPIO MAU-142, MAU-145; Chagos Is., TWCMS C9036–54, C9056, C9062, C9064–5, C9067, C9082, C9083–5, C9092–4, C9096, C12402, C12405–7, C12410; Houtman Albrolhos Is., WAM 389–77, 498–77; Philippines, MP 2504–75, 2567–75; Celebes, MP 1810–76, 1812–76; Kyûsyû, UT 44907 (mentioned Yabe, Sugiyama and Eguchi, 1936, as *Agaricia (?) ponderosa* var. *minikoiensis*, and Ma, 1937, as *Agaricia (Agariciella) minikoiensis);* Solomon Is., WAM 119–77; Bikini Atoll, USNM 44805 (*Leptoseris? mycetoseroides* holotype); Enewetak, EN 1501, 1642, 2207, 2325, 2447, 2918, 2929.

GBR Material: Lizard I. region: Jewell Reef — Outer slope, BM 1979.4.5.2, 1979.4.5.4, 1979.4.5.7, 1979.4.5.14, USNM 54208, QM G12346, G12353, G12358, G12360, G12365–6, G12370–2, G12375, G12380, G12383–4, ZD 9191, 9196, 9200, 9203–4, 9206, 9209–11, 9224, 9230, 9236–8, 9242–5, 9248, 9250, 20304–5. Carter Reef — Outer slope, ZD 9770; Back reef, BM 1979.4.5.11, QM G12363, ZD 9599, 9602, 9604, 9610–11, 9615; Channel to N. of Carter Reef, BM 1979.4.5.8, ZD 10541. Yonge Reef — Outer slope, BM 1979.4.5.12, QM G12343, G12388, G12390, MP 2647, 3317, 3769, ZD 9369, 9824, 20170; Back reef, QM G12373, ZD 9784–6, 10583, 10676; Channel to N. of Yonge Reef, USNM 54205, QM G12381, ZD 9755, 9758, 9762. Unnamed reef S. of Yonge Reef — Channel to N. of reef, QM G21356. S. Ribbon Reef — Back reef, BM 1979.4.5.5, QM G12350, ZD 9311, 9320, 9328, 20268, 20272; Plug Reef, S. end of S. Ribbon Reef, USNM 54206, QM G12378, G12389, ZD 9298, 9301–2, 9304–5, 9307, 9315, 20256. Lizard I. — Area 1, USNM 54207, ZD 9122, 9623; Area 2, BM 1979.4.5.1, QM G12362, G12377, ZD 9591–3, 9992; Area 3, BM 1979.4.5.6, 1979.4.5.10, 1979.4.5.13, 1979.4.5.15, USNM 54209, QM G12341–2, G12349, G12351, G12357, G12361, G12367, G12369, G12382, G12386, MP 3140. ZD: 9339, 9344, 9349–51, 9393, 9806–8, 9810, 9932, 9934, 9936–9, 9982, 9993, 10031, 10078, 10083–4, 10104, 10170, 10227, 10284, 10310, 10346, 10357, 10394, 10402; Area 4, QM G12352, ZD 9389–90, 9621, 9831, 10216–17, 20126, 20306. Nymph I., ZD 9283. Eyrie Reef, QM G12359. MacGillivray Reef, QM G12385. ZD 9280. N. Direction I., QM G12376.

Palm Is. Group: Pelorus I., W. Side, ZD 9505–7, 20307. Curacoa I., SW. side, ZD 20308. Great Palm I., BM 1979.4.5.9, QM G12374, ZD 9541, 20309. Brisk I., QM G12387, ZD 20310. Dido Rock, ZD 20311.

Townsville region: John Brewer Reef, ZD 9554, 9558, 9560, 9562–3. Keeper Reef, ZD 20239.

Heron I. region: Heron Reef — NW. side, BM 1979.4.5.3, QM G12345, ZD 10815; — S. side, QM G12344, G12348, G12354. Wistari Reef, N. side, QM G12347, ZD 10772.

Description

Corallum and Corallites: Corallum most commonly encrusting, sometimes with a free or laminar edge; rarely a plate. Largest specimen collected measures 65 cm by 50 cm, >1 cm thick, but thinner at the margin. Colonies often only a few millimetres thick. Colour: Usually mid-brown, occasionally light or dark brown, or beige. Sometimes green (which may be very bright); or basically brown with patches of another colour, e.g. white, red, beige, or green. Rarely mauve or greyish-brown. Rarely with bright green centres, with or without bright green septocostae.

Corallites usually elliptical, but sometimes round or slightly polygonal, measuring 1·0–7·0 mm (1·0–5·0 mm) by 1·0–4·0 mm (1·0–3·0 mm). Arrangement may depend on development of collines (see below). Corallites flush, somewhat sunken, or near corallum margin sometimes inclined towards margin. Numerous or sparse; where in rows, up to >30 centres per row, but usually <20. Corallites up to >2 cm apart; parent corallite rarely distinguishable.

Collines are a distinctive feature of this species. They may be poorly developed as short, roughly

concentric ridges, or more prominent, bordering long rows of corallites. Concentric collines (those parallel to the corallum margin) may be intersected by other collines, so as to enclose 1–12 (<6) centres, scattered or in short rows. Concentric collines better developed than intersecting ridges; collines often weaker or absent near corallum margin. Here corallites may be inclined towards margin, with proximal cushions as in some other *Leptoseris* species. Collines 1–5 mm (1–3 mm) thick at base, and up to 8 mm above general surface.

SEPTA: Equal or subequal; with profile rounded or acute. Septa non-dentate, imperforate. Number per centre: 6–32 (17).

SEPTOCOSTAE: Equal or subequal; straight, flexuous, or rarely contorted. Upper margin profile usually rounded, sometimes acute. Margin not dentate, but a few specimens have occasional peaks, 0·5–0·75 mm high, extending from the septocostal margin (see Plate 13, fig. 3). These occur only sporadically (not more than once per septocosta on each colline) and have only been found on specimens with large corallites and well developed collines.

Septocostal margin occasionally slightly pitted and discontinuous, especially if septocostae are perforate. However, septocostae normally imperforate. Thickness: Margin: <0·13–0·25 mm (<0·25 mm). Elsewhere: <0·13–0·5 mm (0·25 mm or slightly less). Number in 5 mm: Margin: 22–36 (28). Elsewhere: 14–32 (24).

SURFACE ORNAMENTATION: Sides of septa and septocostae usually with rather rough and fairly profuse granulations. Lateral ridges may be present, but generally more weakly developed than in *L. hawaiiensis*.

FOSSA: Usually elliptical, measuring <0·5–2·0 mm (<1·5 mm) by 0·25–1·0 mm (<0·5 mm). Often shallow.

COLUMELLA: Moderately or well developed; rarely weak, or absent in a few fossae. Usually a round or compressed style; less commonly of loosely fused twisted particles or a boss. Usually most septa reach the columella. However, in a few specimens, about half the septa are much shorter and never reach the columella.

NON-CALICINAL SURFACE: Costae faint, equal or subequal. Number in 5 mm: 20–34 (28). Costal spines, where present, scattered or in rows. Number in 1 mm: 4–10 (7).

HABITAT AND VARIATION

This is one of the commonest species of *Leptoseris*. It occurs on firm substrate, most often in conditions with clear water, but also in turbid water. It can occur unshaded, but most frequently in gullies, overhangs and caves (principally on the ceilings, but also on the side and back walls).

This is undoubtedly the most variable species in the genus, with considerable variation in corallite size, septal number, and size and development of collines. Two extreme forms can be distinguished: coarse forms with large corallites and tall, thick, rounded collines; and fine forms, with smaller corallites, fewer septa and thinner collines. However, the majority of specimens fall between these two extremes, and it seems clear that a single species is involved. Corallite size, septal number and type of colline tend to be relatively consistent within one corallum, i.e. the range of intraspecific variation in these characters is not encountered within a single colony. Coarse and fine forms may be found growing alongside each other, and the differences appear to be genetic. The basic structure of the septa and septocostae remains relatively constant through the series.

Development of collines and corallite shape may be highly variable within one specimen. Some coralla have collines developed all over. But quite commonly, collines are not developed throughout, and about half the colony may lack collines, and may have flush corallites, or 'normal' *Leptoseris* corallites with proximal cushions. The reasons for this variation are not clear. However, some specimens have been found with collines best developed on the most illuminated parts of the corallum, while thinner, laminar areas without collines occur on more shaded parts of the colony.

DISTRIBUTION

Indo-Pacific: Madagascar; Reunion; Mauritius; Saya de Malha; Chagos Archipelago; Houtman Abrolhos Is.; Indonesia; Philippines; Celebes; Kyûsyû; Honsyû; Great Barrier Reef; Solomon Is.; Marshall Is.

BATHYMETRIC RANGE: 3–46 m (GBR); 23–80 m (at Bikini, Wells 1954).

AFFINITIES

As already noted, certain specimens which lack collines may come close to *L. hawaiiensis*. *L. mycetoseroides* has similar septa and septocostae to those of *L. foliosa*, but in the latter species they are much more granulated, and the species are easily separated on growth form alone.

Previous workers have been in doubt as to the generic position of this species, as discussed in the history of the genus. However, apart from the presence of collines, this species has much closer affinities with other *Leptoseris* than with species in other genera.

Leptoseris foliosa n. sp.
(Plate 14)

Leptoseris tenuis: Yabe and Sugiyama, 1941, p. 74, pl. 62, figs. 4–4c, 5–5a, pl. 64, fig. 1. Veron and Pichon, 1979, p. 65, figs. 115–20, 742.
not *Leptoseris tenuis* van der Horst, 1921, p. 31, pl. 5, figs. 9, 10; 1922, p. 422.

HOLOTYPE
Lizard I., Area 1 (lagoon), 8 m, M. Pichon, November 1977, BM 1979.4.6.1.

PARATYPES
Lizard I. region: Turtle Is., W. side, BM 1979.4.6.5–6. Lizard I. — Area 1, BM 1979.4.6.3–4, QM G12391–2, G12396–7, ZD 9069, 9944; Area 2, QM G12395, G12398; Area 4, BM 1979.4.6.2.
Palm Is. Group: Pelorus I., W. side, QM G12394. Great Palm I., S. side, QM G12393. Esk I., N. side, USNM 54200, ZD 9503.

DIAGNOSIS
Corallum usually encrusting at base, with upper part foliose. Corallites small, superficial, slightly sunken, often it short rows. Septa and septocostae equal, close, non-dentate, very well granulated. Columella well developed, usually a style or boss, fossa small and shallow.

DESCRIPTION
CORALLUM AND CORALLITES: Corallum usually with encrusting base, with the upper part foliose, often fan-shaped. Margin often very curved, and may curl round to form tubes, up to 4 cm wide. Rarely a plate. Largest colony collected measures 12 cm high, 5 cm wide at the base, 13·5 cm across the broadest part of the fan. Thickness at base approaching 1 cm, but <1 mm at margin. Colour: Dark and light brown.

Corallites often very elliptical, measuring 1·0–4·0 mm (1·0–2·0 mm) by 1·0–2·0 mm (1·0–1·5 mm). Corallites superficial and poorly delineated, usually slightly sunken in; scattered or in short rows, with up to nine centres per row. Usually crowded, but rows or corallites up to 1 cm apart. Proximal cushions never present. Occasional, peak-shaped nodules up to 4 mm high. Parent corallite rarely distinguishable.

SEPTA: Equal, close, often with rounded profile. Septa non-dentate, imperforate. Number per centre: 8–28 (18).

SEPTOCOSTAE: Equal, close, usually fairly straight, sometimes contorted especially on encrusting parts. Upper margin profile normally rounded; rarely with a narrow ridge down the centre. Septocostae non-dentate, imperforate. Thickness: Margin: <0·13–0·25 mm (<0·25 mm). Elsewhere: <0·13–0·38 mm (0·25 mm). Number in 5 mm: Margin: 20–30 (24). Elsewhere: 18–28 (21).

SURFACE ORNAMENTATION: Surface of septa and septocostae very well granulated, granulations rough and very profuse. Lateral ridges weakly developed or absent.

FOSSA: Usually elliptical, measuring <0·25–1·25 mm (0·5–0·75 mm) by <0·25–0·5 mm (<0·5 mm). Very shallow.

COLUMELLA: Rather well developed, a style or boss, often with uneven, sculptured surface; occasionally a looser structure of particles in a row. Most or all septa reach the columella.

NON-CALICINAL SURFACE: Costae very faint, equal or subequal. Number in 5 mm: 18–28 (22). Costal spines small, often scattered over costae. Number in 1 mm: 6–10 (8).

HABITAT AND VARIATION
Most specimens were collected in turbid water conditions on soft bottoms (fine sand or mud) but attached to a piece of substrate, in shallow water in the vicinity of fringing reefs. The erect growth form may help to reduce the effects of sedimentation. The only plate-shaped specimen was collected in more exposed conditions, in deeper water (20 m) from a cave. Poor illumination may explain its different growth form.

Most specimens are very consistent in general growth form, although the shape of the upper, foliose part is somewhat variable. Corallite size and arrangement, structure of septa and septocostae, and columellar development are remarkably consistent.

DISTRIBUTION
Indo-Pacific: Great Barrier Reef and Solomon Is.

BATHYMETRIC RANGE: 8 – 20 m (GBR).

AFFINITIES

This species is most closely related to forms of *L. mycetoseroides* with small corallites. The septa and septocostae are very similar, but much more granulated in the new species. *L. foliosa* is easily distinguished by its growth form, and by the quite different arrangement of the corallites.

DISCUSSION

Yabe and Sugiyama referred their specimen (UT 62526) to *Leptoseris tenuis* van der Horst. The specimen marked 'type' of *L. tenuis* (AM Coel 695), loaned from the Zoölogisch Museum, Amsterdam, is clearly not the holotype illustrated by van der Horst (1921, pl. 5, figs. 9, 10), and the type appears to have been lost. Specimen AM Coel 695 is a *L. hawaiiensis,* as are two other specimens (AM Coel 696, BM 1937.11.17.73) from the Percy Sladen Expedition, identified by van der Horst, and mentioned by him (1922, p. 422). A further specimen (BM 1937.11.17.101) from the same expedition, also identified and mentioned by van der Horst, is a *L. mycetoseroides*. Van der Horst's descriptions and figures (1921; 1922) of *L. tenuis* certainly do not suggest that it is the same as *L. tenuis sensu* Yabe and Sugiyama, 1941. Hence *L. foliosa* is here described as a new species.

Leptoseris glabra, n. sp.
(Plates 15–16)

Leptoseris cf. *hawaiiensis:* Yabe and Sugiyama, 1941, p. 73, pl. 62, figs. 3–3d.

Leptoseris explanata: Veron and Pichon, 1979, p. 42, figs. 71–82, 738.

not *Leptoseris hawaiiensis* Vaughan, 1907, p. 137, pl. 39, pl. 40.

not *Leptoseris explanata* Yabe and Sugiyama, 1941, p. 75, pl. 63, figs. 3–3e.

HOLOTYPE

Palm Is. Group, Pelorus I., W. side, 17 m, Z. Dinesen, April 1976, BM 1979.4.7.1.

PARATYPES

NON-GBR MATERIAL: Red Sea, Eilat, UTA NS10749; Reunion, GF REU.503; Houtman Abrolhos Is., WAM 390–77; Solomon Is., WAM 116–77; Palau, UT 60635 (mentioned Yabe and Sugiyama, 1941, as *Leptoseris* cf. *hawaiiensis*).

GBR MATERIAL: Lizard I. region: Jewell Reef — Outer slope, BM 1979.4.7.10, QM G12413, G12418, ZD 20288. Carter Reef — Knoll, back reef, QM G12420, ZD 9597; Channel to N. of Carter Reef, BM 1979.4.7.5, QM G12403, G12421, ZD 9765, 10537; Channel to S. of Carter Reef, QM G12410. Yonge Reef — Outer slope, ZD 9790; Back reef, QM G12415, G12422, ZD 9568–9, 9571; Channel to N. of Yonge Reef, BM 1979.4.7.2, 1979.4.7.6, USNM 54199, QM G12404, ZD 9760, 10919. Unnamed reef S. of Yonge Reef — Channel to N. of reef, QM G12412, G12424. S. Ribbon Reef — Plug Reef at S. end, QM G12402, G12406. Lizard I. — Area 2, BM 1979.4.7.3, ZD 9583.

Palm Is. Group: Pelorus I., W. side, BM 1979.4.7.7, QM G12407, G12416, G12419, ZD 9846. Orpheus I., Pioneer B., BM 1979.4.7.9, USNM 54198, QM G12401, G12405, G12411, G12414, G12417, G12423, ZD 9496, 9875, 9879, 9882, 9889. Curacoa I., SW. side, QM G12399, G12408. Eclipse I., BM 1979.4.7.4. Esk I., S. side, BM 1979.4.7.8. Brisk I., QM G12409. Dido Rock, QM G12400.

DIAGNOSIS

Corallum plate- or bowl-shaped; partly encrusting; or erect with foliose margin, often dissected into wide fronds. Corallites large and elliptical with wide fossae and numerous septa. Septa and septocostae strongly alternating, those of the first order being thicker and much more exsert. Septocostal margin typically smooth. Columella usually well developed, a solid boss or twisted particles, more or less fused.

DESCRIPTION

CORALLUM AND CORALLITES: Corallum plate- or bowl-shaped; encrusting with free margin; or erect with foliose margin, which may be divided into wide fronds. Fronds usually several centimetres across, but may be <2 cm wide where recently divided. Fronds flat, or curled around to form low tubes, up to about 3 cm across. Margin may be reflected onto non-calicinal surface for up to 2 cm and corallites may develop here so that, at the margin, corallum appears bifacial. (See Plate 16, fig. 2.) Largest specimen collected measures 47 cm by 35 cm, >1 cm thick, but <1 mm at the margin. Colour: Usually brown or beige, sometimes green, or brown with beige. Often a white margin; sometimes paler septa and septocostae.

Corallites usually elliptical and large, measuring 2·0–12·0 mm (5·0–8·0 mm) by 2·0–6·0 mm (3·0–5·0 mm). Sometimes almost flush, but usually inclined towards corallum margin. Parent

corallite sometimes distinguishable. Corallites numerous to sparse, scattered or in roughly concentric rows, with up to 25 centres per row. Corallites or rows adjacent to over 6 cm apart. Proximal cushions up to 6 mm high.

SEPTA: Usually strongly alternating, with those of the first order thicker and more exsert. Profile usually rounded. Margin non-dentate; septa imperforate. Number per centre: 10–50 (30).

SEPTOCOSTAE: As septa, usually strongly alternating, even at corallum margin. Straight or slightly flexuous, rarely contorted over raised areas of corallum. Upper margin profile of first order septocostae normally rounded; margin of second order septocostae flatter, often with a narrow ridge running down the centre. Margin non-dentate; septocostae nearly always imperforate. A few specimens have a slightly pitted and discontinuous septocostal margin, and some perforations in the septocostae. Occasionally three orders of septocostae can be distinguished. Thickness: Margin (first order septocostae): 0·13–0·5 mm (0·38 mm). Margin (second order septocostae): <0·13–0·38 mm (0·25 mm). Elsewhere (first order septocostae): 0·13–0·75 mm (0·5 mm). Elsewhere (second order septocostae): <0·13–0·5 mm (0·38 mm). Number in 5 mm: Margin: 12–20 (16). Elsewhere: 11–18 (14).

SURFACE ORNAMENTATION: Surface of septa and septocostae, especially those of first order, well granulated; granulations often coalesce to form sharp, wavy ridges, these being more conspicuous than in other species. Lateral ridges prominent on second order septocostae.

FOSSA: Usually elliptical, measuring 0·75–6·0 mm (1·5–4·0 mm) by <0·5–1·0 mm (0·5 mm). Shallow to over 3·0 mm deep in prominent corallites.

COLUMELLA: Usually well developed, elliptical to fit shape of fossa. Often a solid boss with uneven, sculptured surface; sometimes of twisted particles, more or less fused. Few to most septa may reach columella; in general, most first order septa reach columella, most second order septa do not.

NON-CALICINAL SURFACE: Costae, when present, usually equal. Number in 5 mm: 10–22 (15). Costal spines may be scattered or in a row along each costa. Number in 1 mm: 5–9 (7).

HABITAT AND VARIATION

Specimens have been collected principally from two very different biotopes. Those from protected areas, with high sedimentation rates and turbid water, may be found on muddy bottoms. They are usually erect, somewhat foliose, sometimes tubuliferous. This growth form may help to reduce the effects of sedimentation. Specimens from Outer Barrier localities, found on firm substrate, are usually plate-shaped or partly encrusting. They have been found unshaded, but more often in gullies and caves (on the ceiling or floor).

Apart from the growth form, there is also some variation in corallite size and septal number. In general, the structure of the septa and septocostae, and the columella, are rather consistent. A few specimens have been found with rather more equal septa and septocostae, and this condition may sometimes be associated with poor illumination.

DISTRIBUTION

Indo-Pacific: Red Sea; Reunion; Houtman Abrolhos Is.; Great Barrier Reef: Solomon Is.; Palau.

BATHYMETRIC RANGE: 5–44 m (GBR); 110 m (at Palau, Yabe and Sugiyama 1941).

AFFINITIES

This species is most closely related to *L. gardineri*. However, coralla of *L. gardineri* have narrow branches, with generally smaller corallites and fewer septa. The septa and septocostae, though of similar structure, are less alternating in *L. gardineri*.

As previously discussed, *L. glabra* also has some affinities with *L. scabra* and *L. solida*.

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PLATE 1

FIG. 1: *Leptoseris cucullata* (Ellis and Solander, 1786). × 0·9. Belize, Carrie Bow Cay, USNM 47321.

FIGS. 2, 3: *L. cucullata*. × 0·8; × 3·4. Jamaica, DB 2432.

FIG. 4: *Leptoseris papyracea* (Dana, 1846). × 4·4. Macclesfield Bank, BM 1892.10.17.130 (piece of holotype of *Pavonia ramosa*).

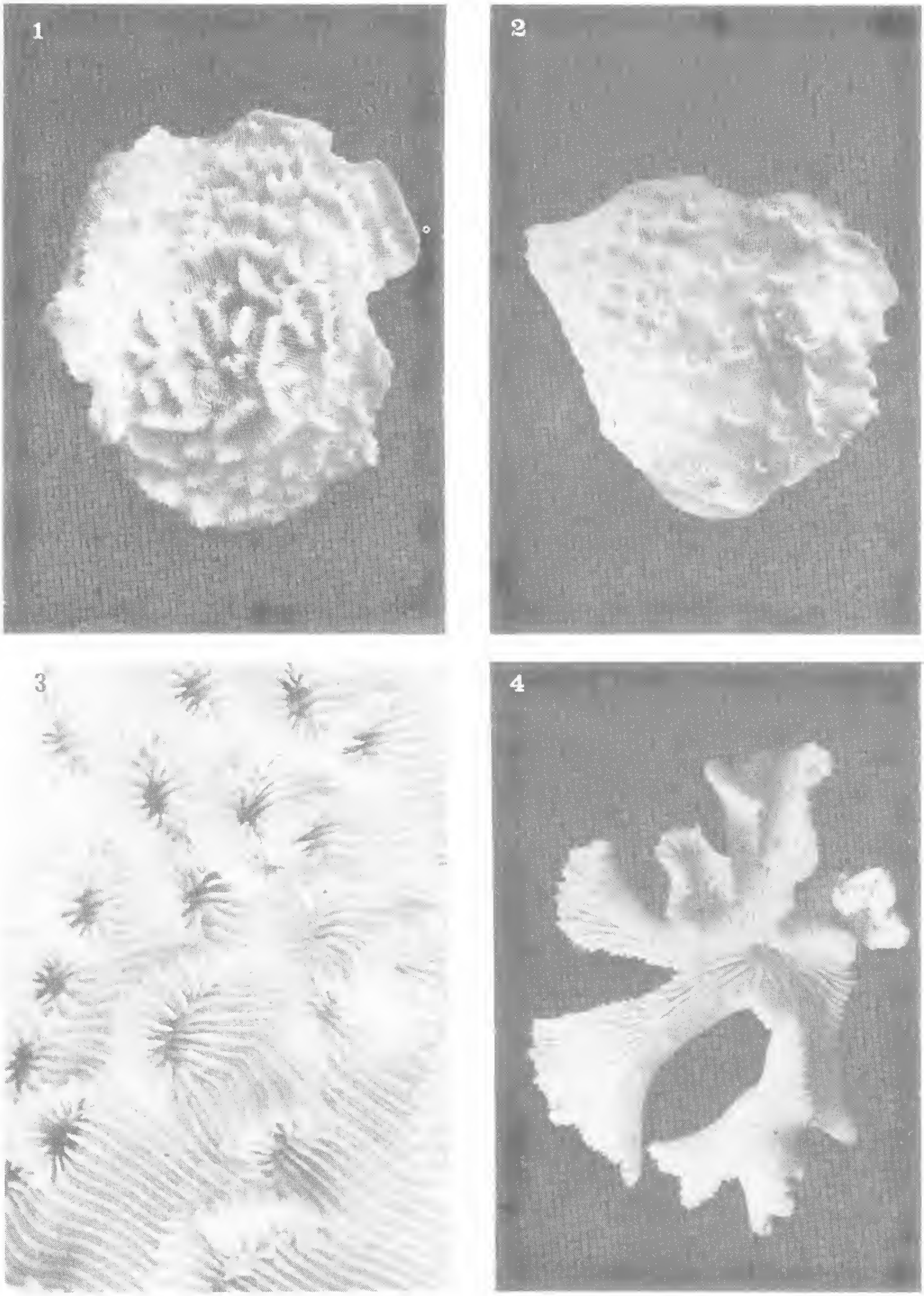
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PLATE 2

FIG. 1: *Leptoseris papyracea* (Dana, 1846). × 3. Tizard Bank, BM 16B (*Pavonia pretiosa* holotype).

FIG. 2: *L. papyracea*. × 1·5. 19°01'S, 146°58'E, (off Townsville), GBR, 25 m, ZD 20292.

FIGS. 3, 4: *Leptoseris cailleti* (Duchassaing and Michelotti, 1864). × 2·8; × 0·6. Off Mayagüez, Puerto Rico, USNM 54215.

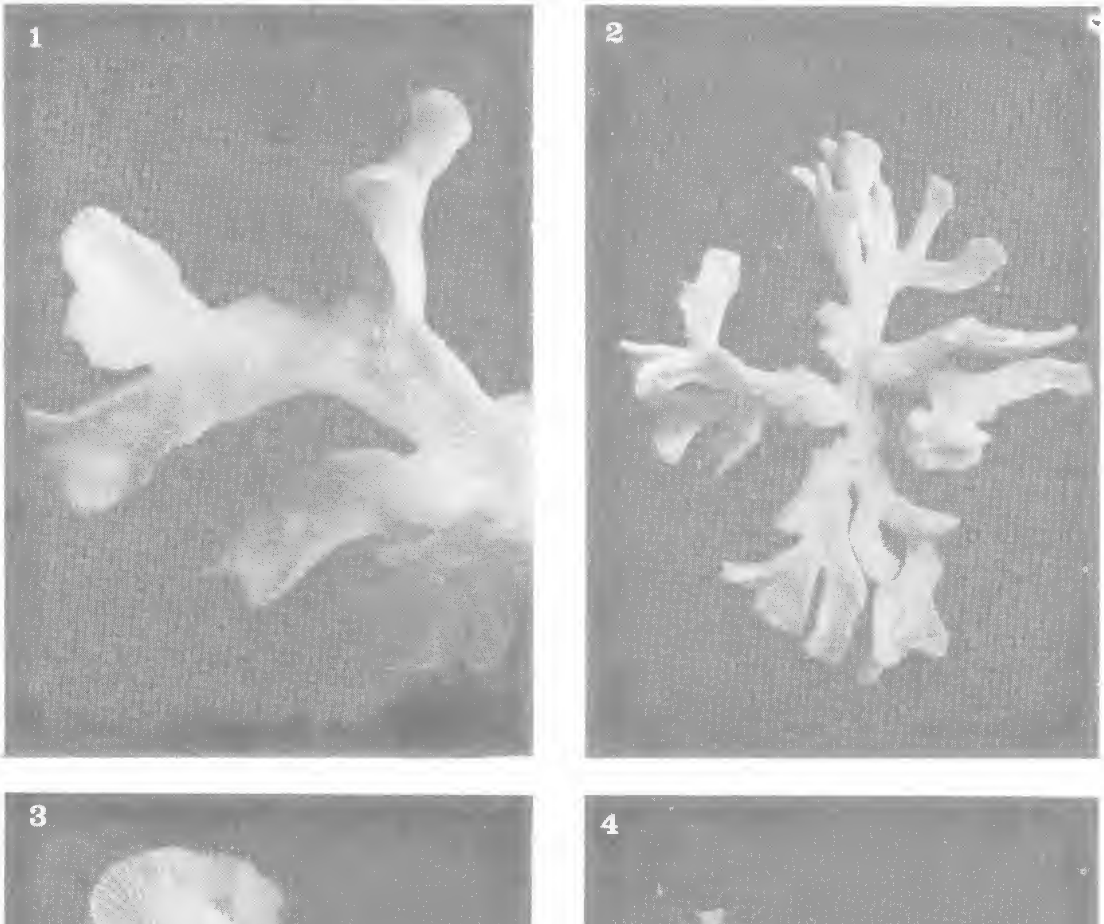
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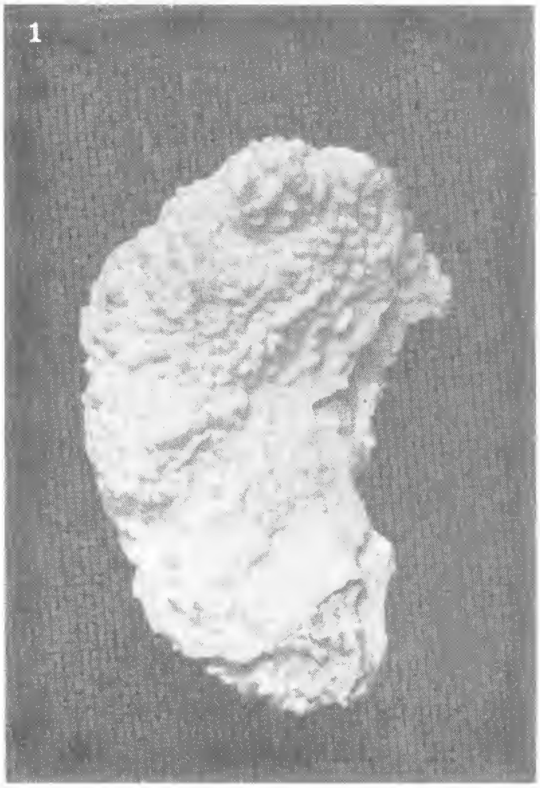
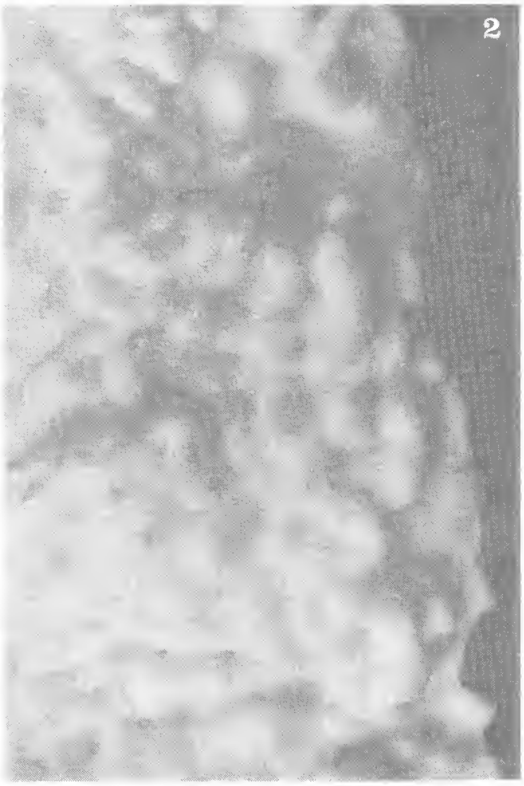
PLATE 3

FIGS. 1, 2: *Leptoseris incrustans* (Quelch, 1886). × 0·7; × 2·9. Tahiti, BM 1886.12.9.172 (*Cylloseris incrustans* cotype).

FIG. 3: *Leptoseris solida* (Quelch, 1886). × 0·4. Tahiti, BM 1886.12.9.177 (*Domoseris solida* holotype).





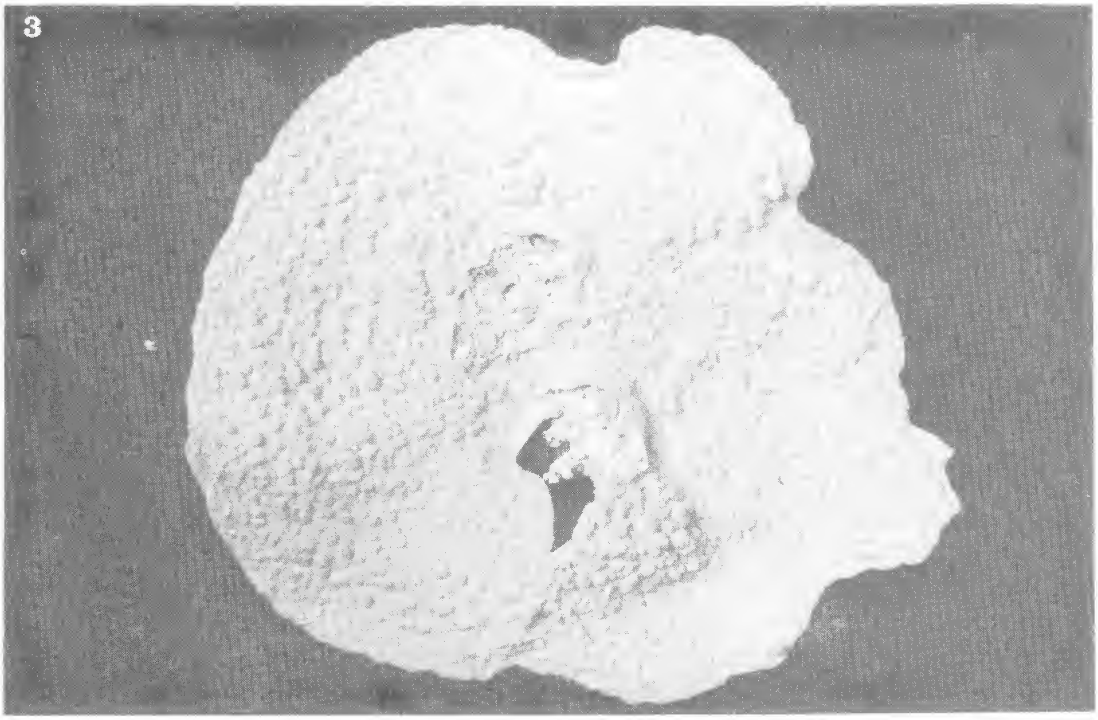


PLATE 4

FIG. 1: *Leptoseris solida* (Quelch, 1886). × 3. Tahiti, BM 1886.12.9.177. (*Domoseris solida* holotype).

FIG. 2: *L. solida*. × 1. Tahiti, BM 1886.12.9.296 (*Domoseris porosa* holotype).

FIG. 3: *L. solida*. × 3. Easter I, USNM 53156 (piece of holotype of *L. paschalensis*).

FIG. 4: *Leptoseris hawaiiensis* Vaughan, 1907. × 1·5. Hawaii, USNM 20875 (*L. hawaiiensis* cotype).

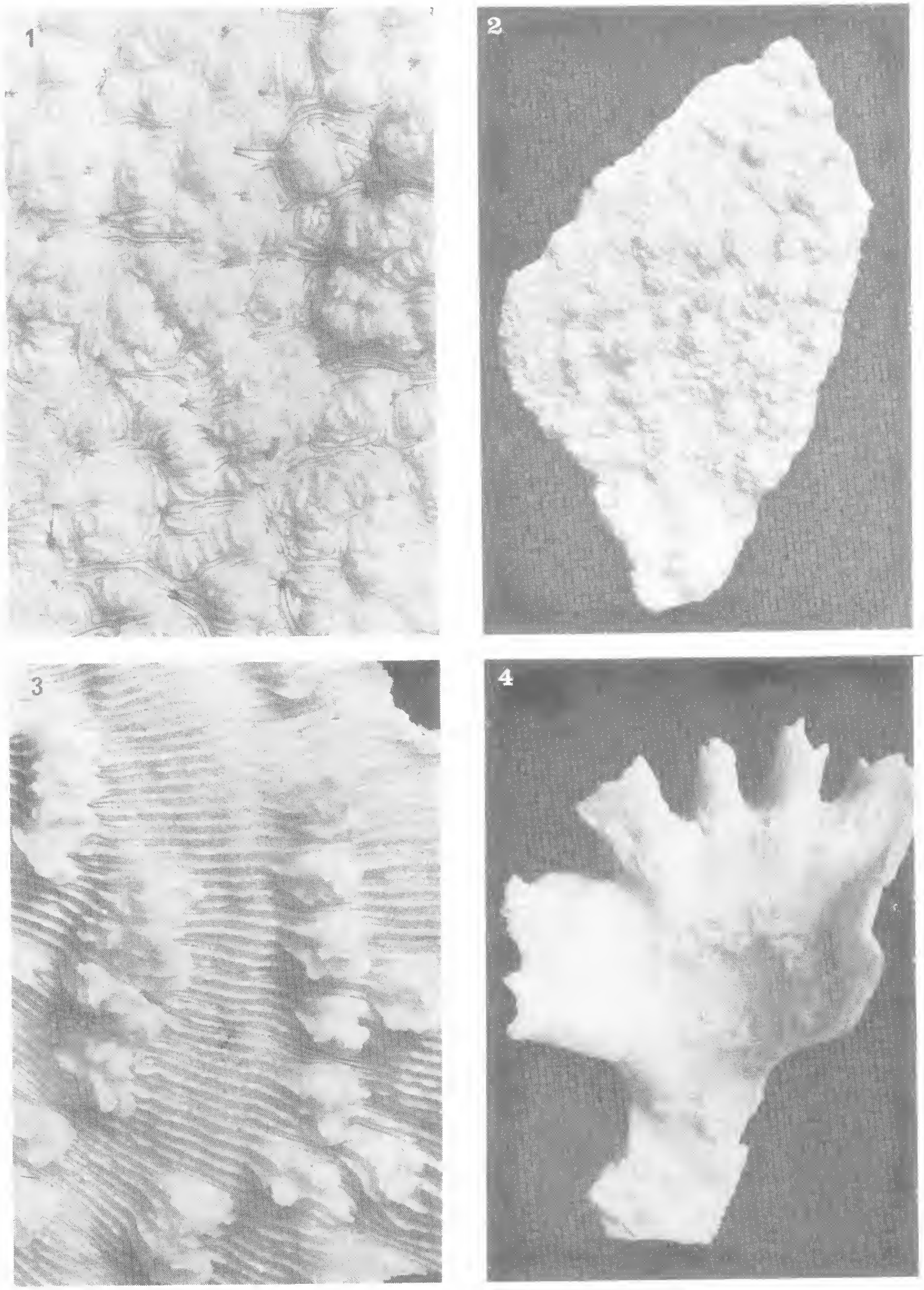

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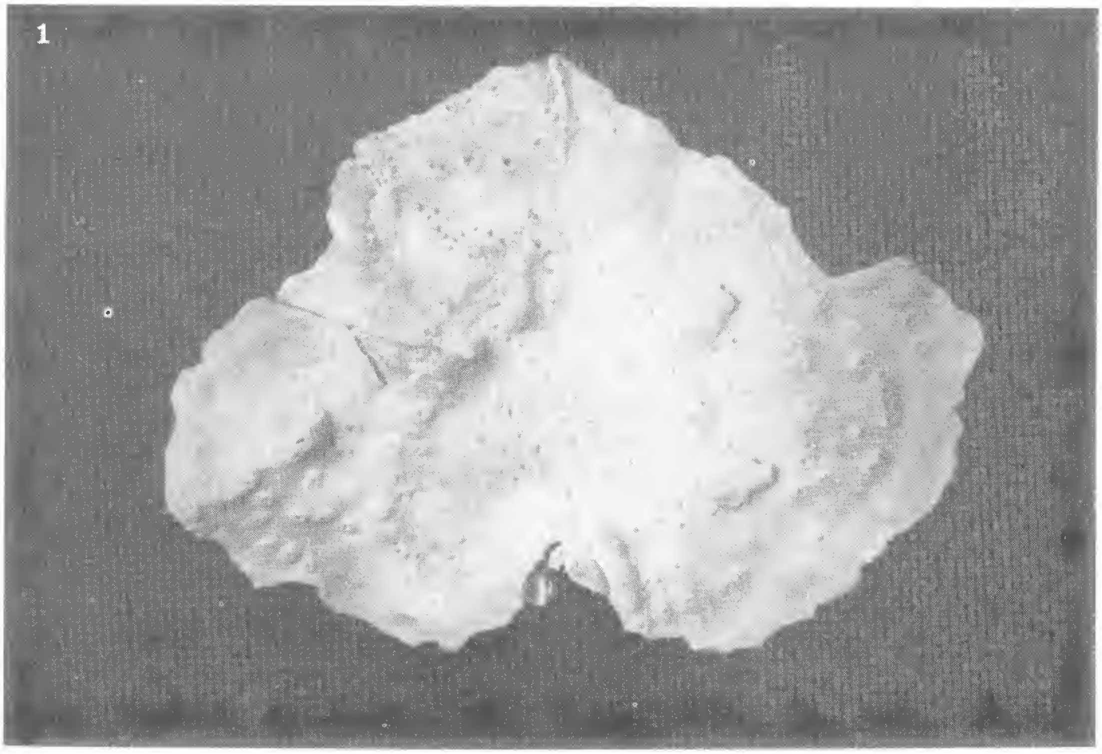
PLATE 5

FIGS. 1, 2: *Leptoseris hawaiiensis* Vaughan, 1907. × 0·6; × 3·4. USNM 20843 (*L. hawaiiensis* cotype).

FIG. 3: *L. hawaiiensis*. × 1·6. Borneo, BM 1851.1.20–12 (*L. striatus* holotype).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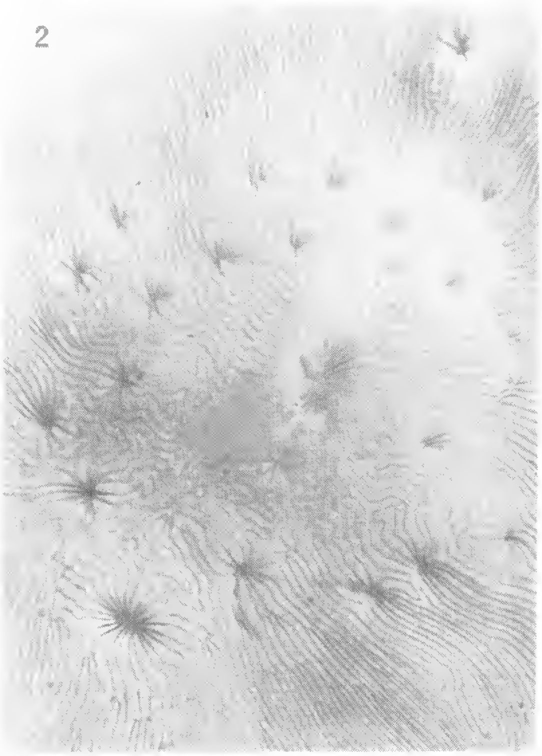
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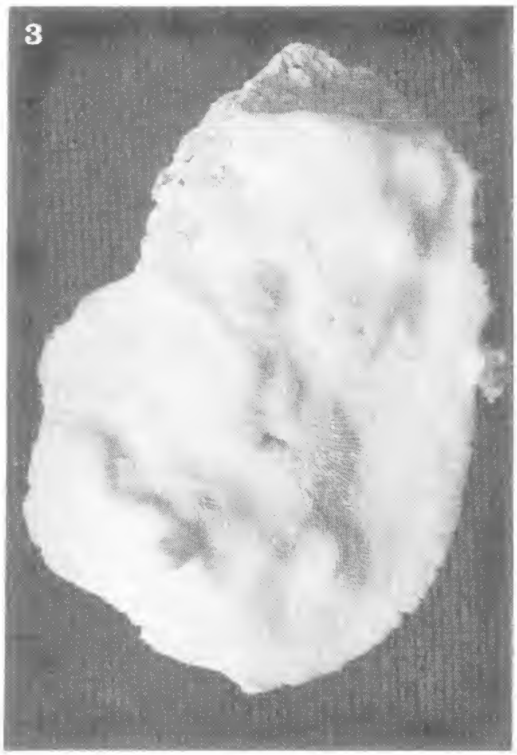
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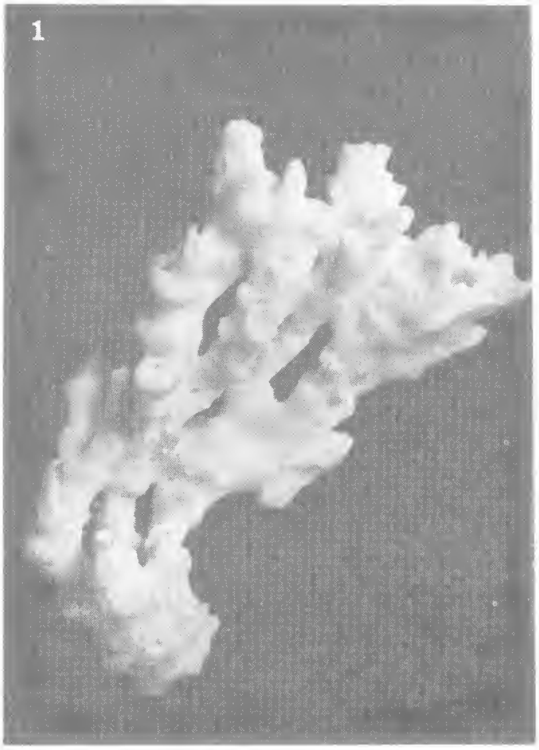
PLATE 6

FIG. 1: *Leptoseris hawaiiensis* Vaughan, 1907. × 1·3. Hawaii, USNM 20846 (*L. tubulifera* cotype).

FIG. 2: *L. hawaiiensis*. × 3·3. Maldives, CM Registered but not numbered (*L. incrustans* Gardiner holotype).

FIG. 3: *L. hawaiiensis*. × 3. Amirante Is, BM 1937.11.17.123 (*L. gravieri* holotype).

FIG. 4: *L. hawaiiensis*. × 3. Channel to N. of Carter Reef, GBR, 5 m, ZD 9769.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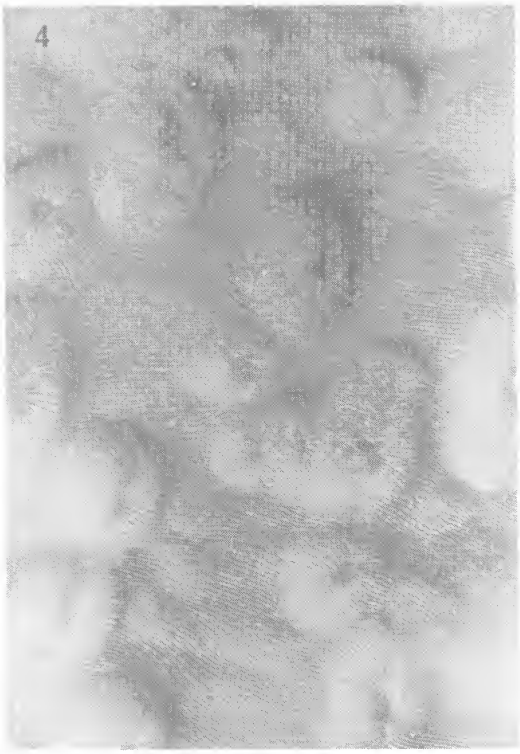
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PLATE 7

FIG. 1: *Leptoseris hawaiiensis* Vaughan, 1907. × 3. Outer slope, Carter Reef, GBR, 8 m, ZD 9840.

FIG. 2: *L. hawaiiensis*. × 3. Back reef, Yonge Reef, GBR, 6 m, ZD 9570.

FIG. 3: *L. hawaiiensis*. × 0·6. Channel to N. of Carter Reef, GBR, 5 m, ZD 9769.

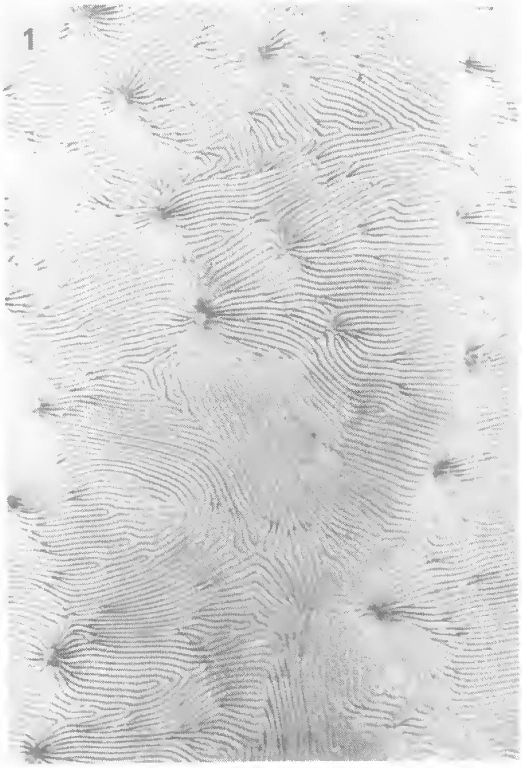
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PLATE 8

FIG. 1: *Leptoseris scabra* Vaughan, 1907. × 2·9. Hawaii. USNM 20886 (*L. scabra* cotype).

FIG. 2: *L. scabra*. × 1. Tahiti, BM 1886.12.9.295 (*Domoseris regularis* cotype).

FIG. 3: *L. scabra*. × 1·3. Lizard I., Area 2, GBR, 12 m, ZD 9273.


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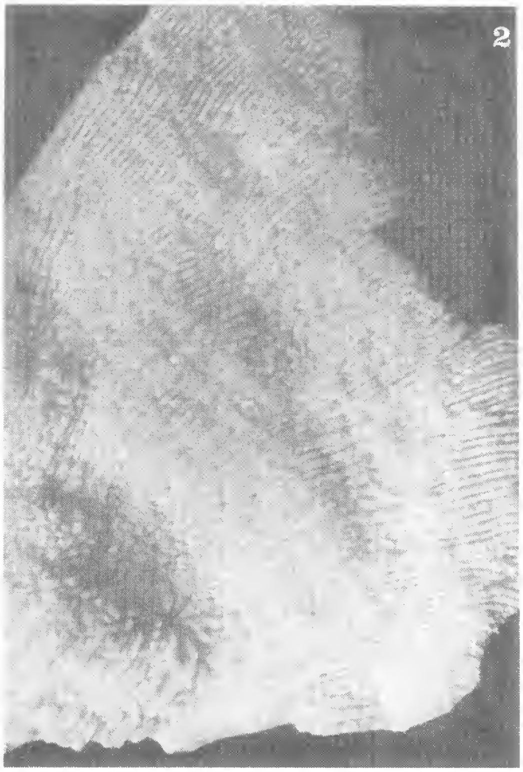
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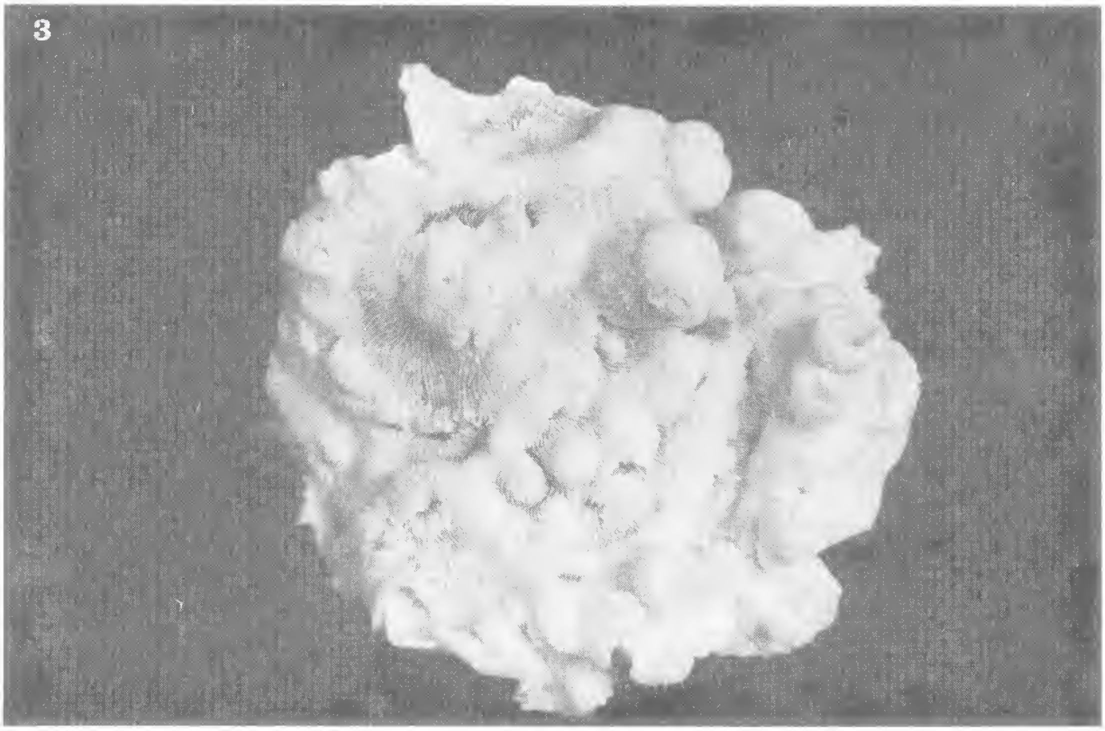
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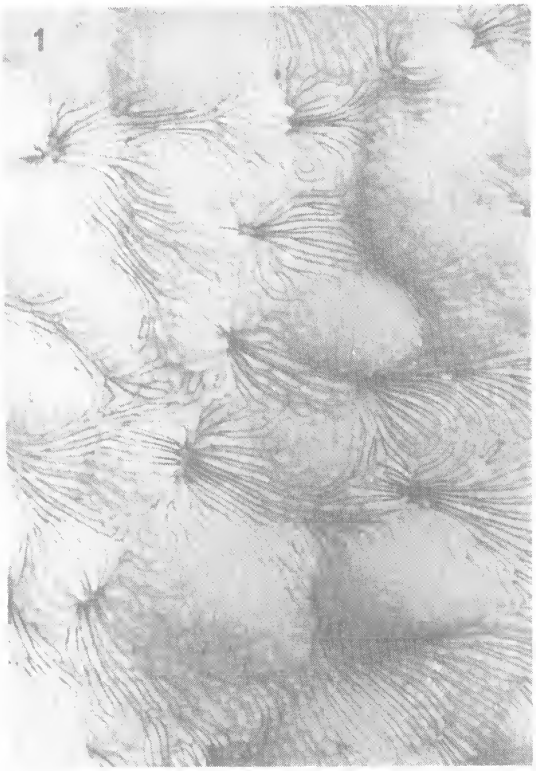
PLATE 9

FIG. 1: *Leptoseris scabra* Vaughan, 1907. × 3. Lizard I., Area 2, GBR, 12 m, ZD 10215.

FIGS. 2, 3: *L. scabra*. × 3; × 1. Back reef, Carter Reef, GBR, 10 m, ZD 9613.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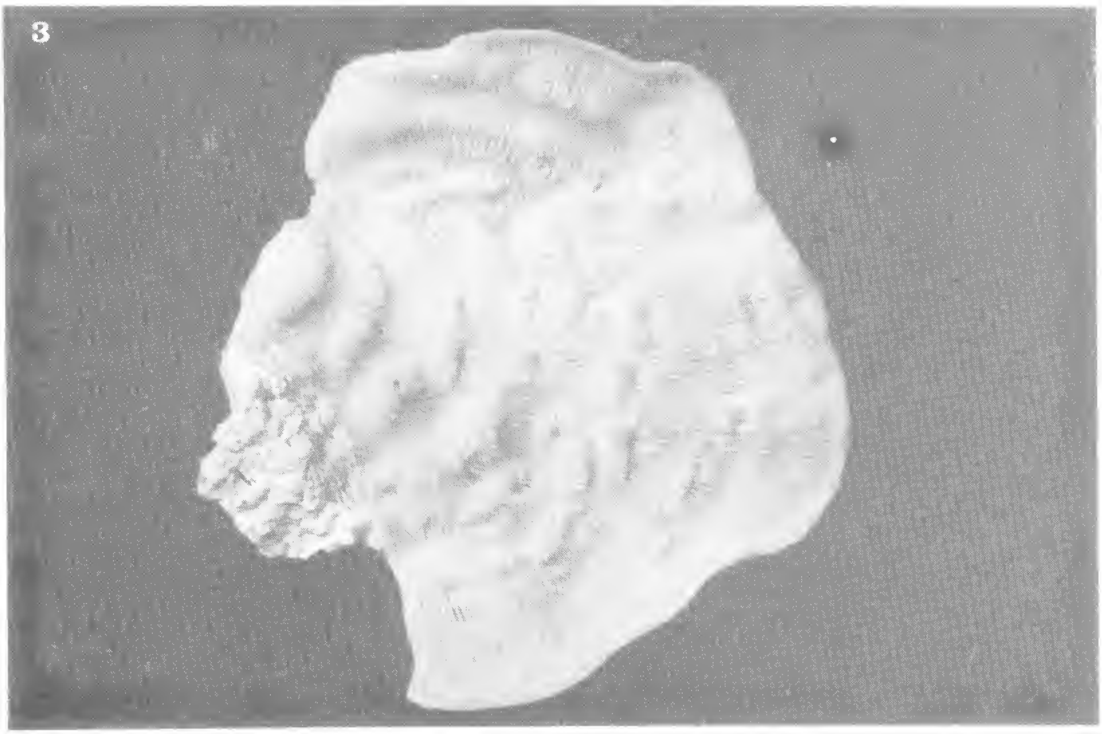
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PLATE 10

FIG. 1: *Leptoseris gardineri* van der Horst, 1921. × 2·9. Orpheus I., Pioneer B., Palm Is. Group, GBR, 15 m, ZD 9893.

FIGS. 2, 3: *L. gardineri*. × 3; × 0·6. Pelorus I., W. side, Palm Is. Group, GBR, 18 m, ZD 9538.


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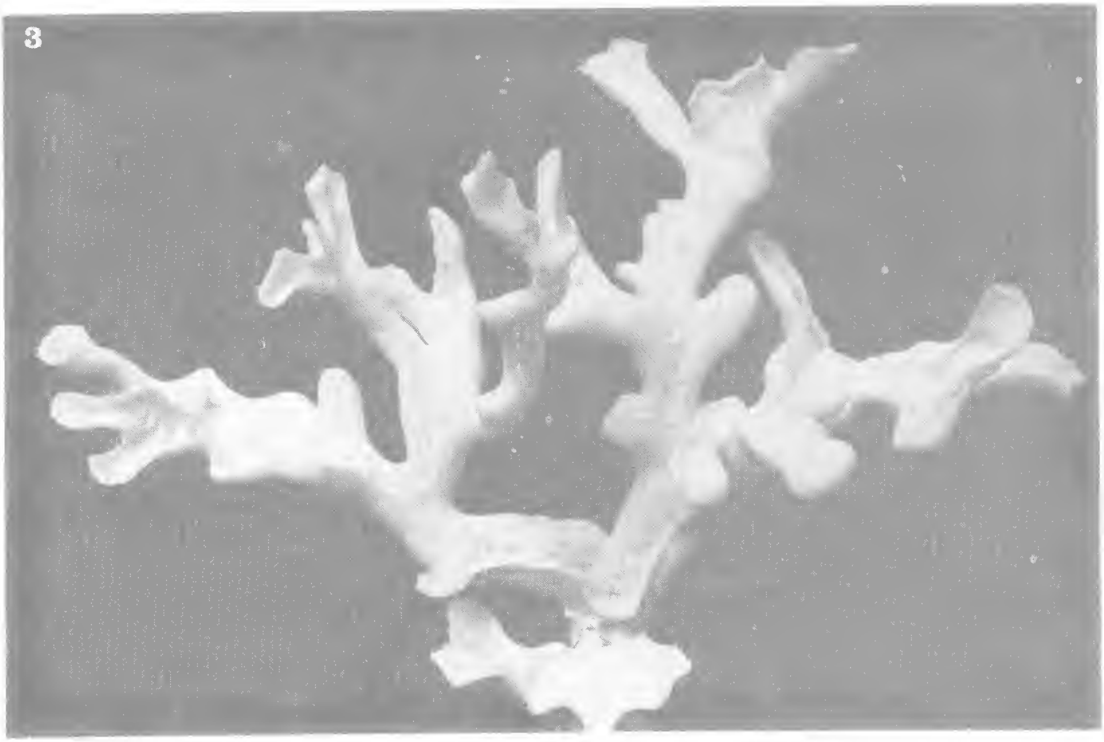
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PLATE 11

FIGS. 1, 2: *Leptoseris mycetoseroides* Wells, 1954. × 0·5; × 3. Bikini Atoll, USNM 44805 (*L.? mycetoseroides* holotype).
FIG. 3: *L. mycetoseroides*. × 0·7. Kyûsyû, UT 44907.

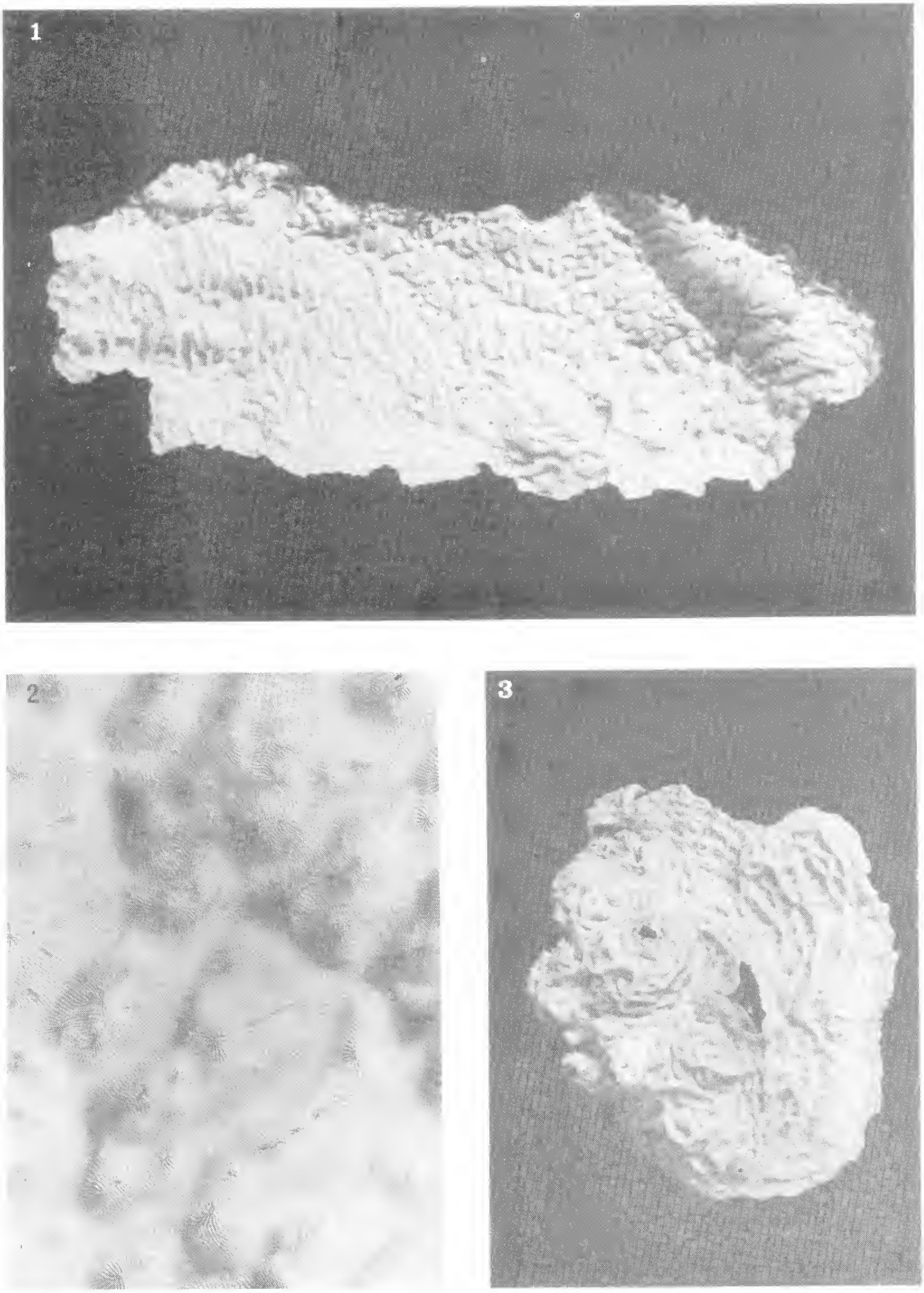
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PLATE 12

FIG. 1: *Leptoseris mycetoseroides* Wells, 1954. × 3. Outer slope, Jewell Reef, GBR, 15 m, ZD 9224.

FIGS. 2, 3: *L. mycetoseroides*. × 3·3; × 0·5. Back reef, Carter Reef, GBR, 8 m, ZD 9615.

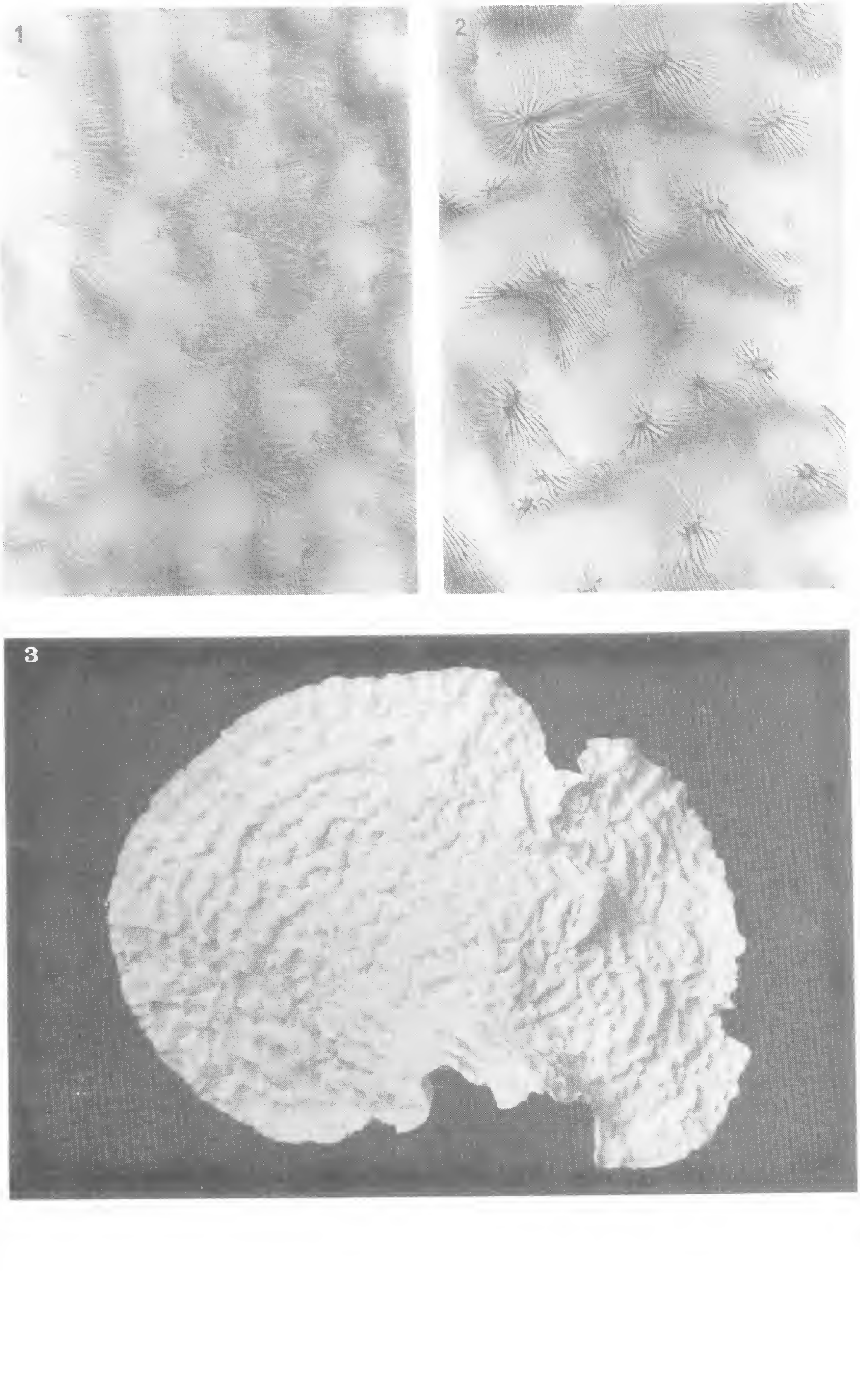
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PLATE 13

FIGS. 1, 2: *Leptoseris mycetoseroides* Wells, 1954. × 0·6; × 3. Outer slope, Yonge Reef, GBR, 40–56 m, MP 3679.

FIG. 3: *L. mycetoseroides*. × 3·8. John Brewer Reef, GBR, 9 m, ZD 9554.

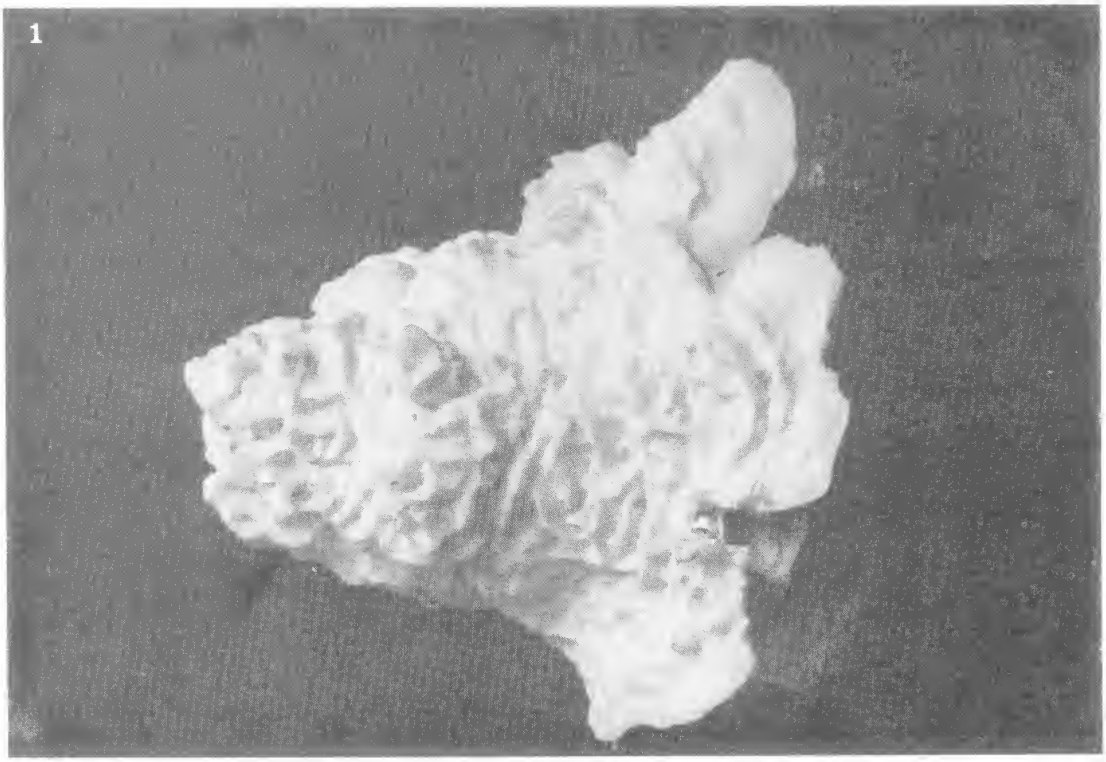
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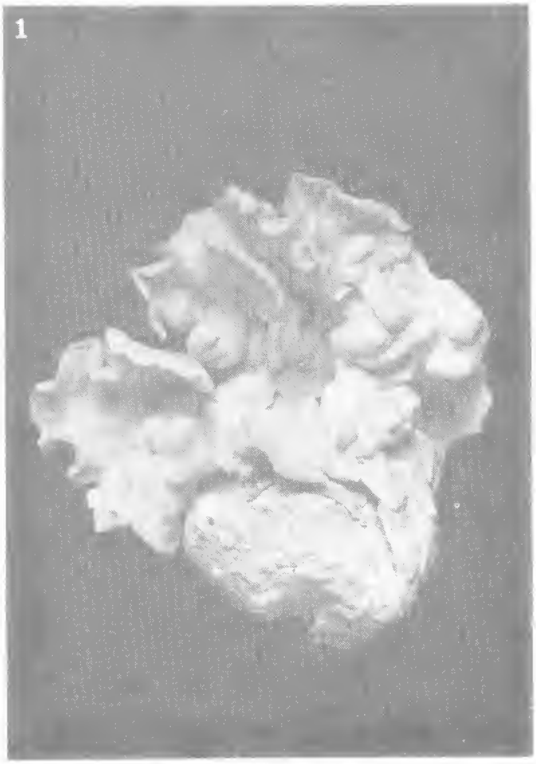
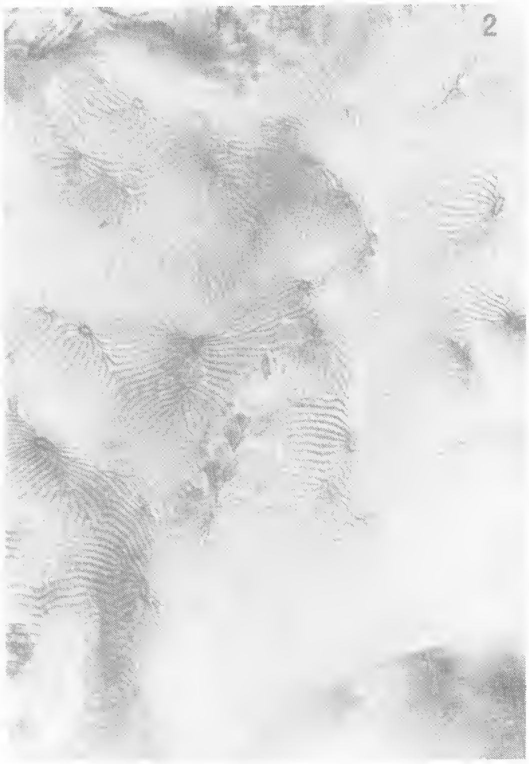
PLATE 14

FIGS. 1, 2: *Leptoseris foliosa* n. sp. × 0·7; × 3·9. Lizard I., Area 1, GBR, 8 m, BM 1979.4.6.1. (holotype).

FIG. 3: *L. foliosa*. × 0·8. Lizard I., Area 1, GBR, 5–10 m. BM 1979.4.6.3. (paratype).





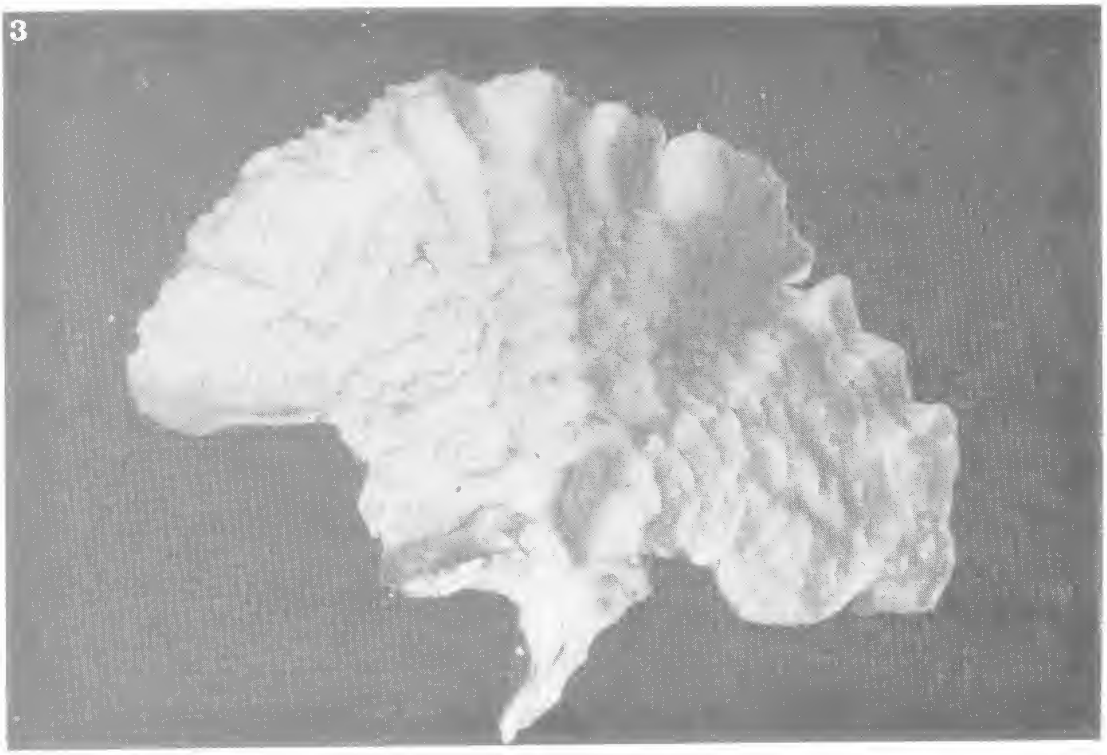


PLATE 15

FIGS. 1, 2: *Leptoseris glabra*, n. sp. × 0·7; × 3. Pelorus I., W. side, Palm Is. Group, GBR, 17 m, BM 1979. 4.7.1 (holotype).

FIG. 3: *L. glabra*. × 3·2. Orpheus I., Pioneer B., Palm Is. Group, GBR, 14 m, ZD 9496 (paratype).

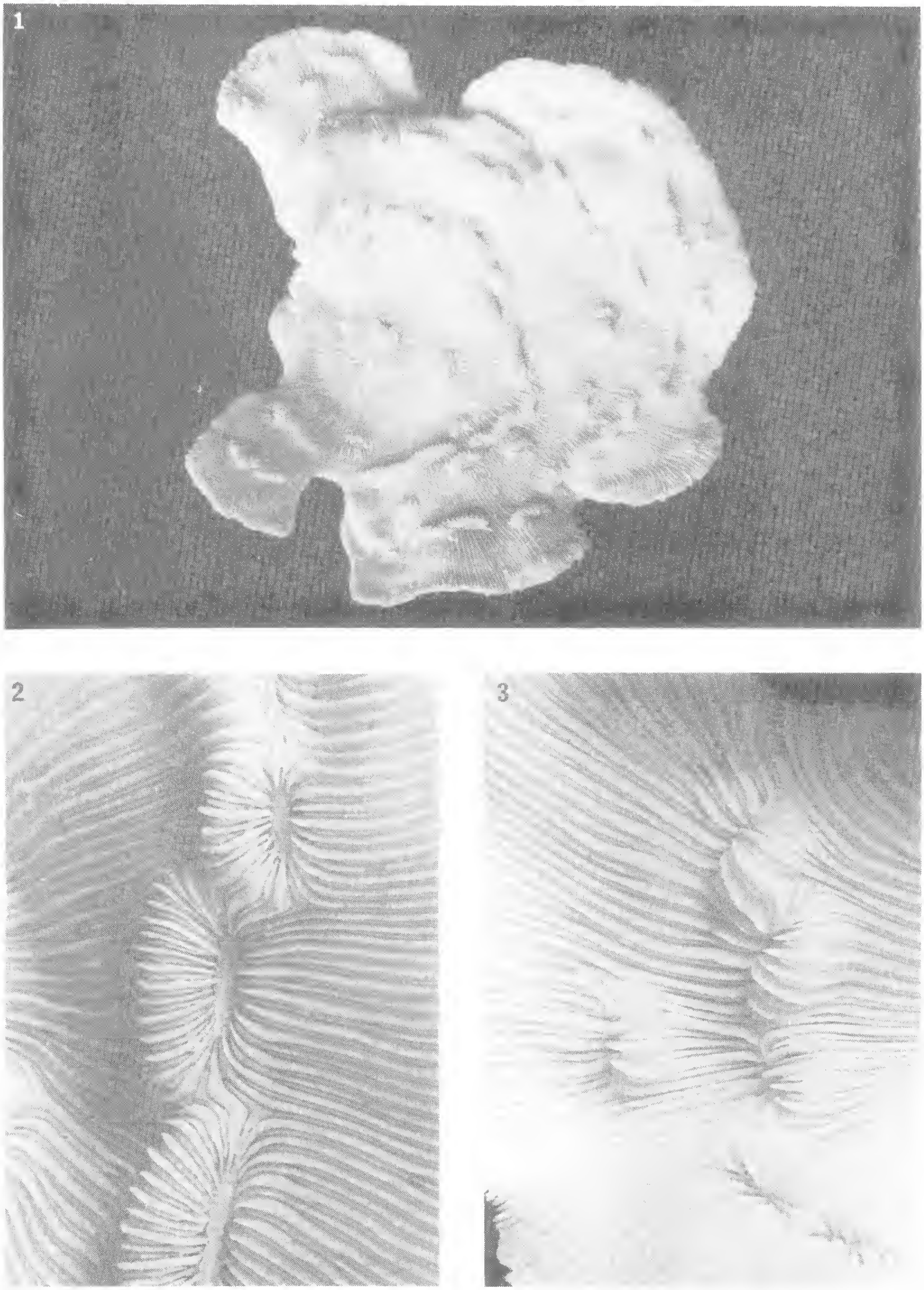

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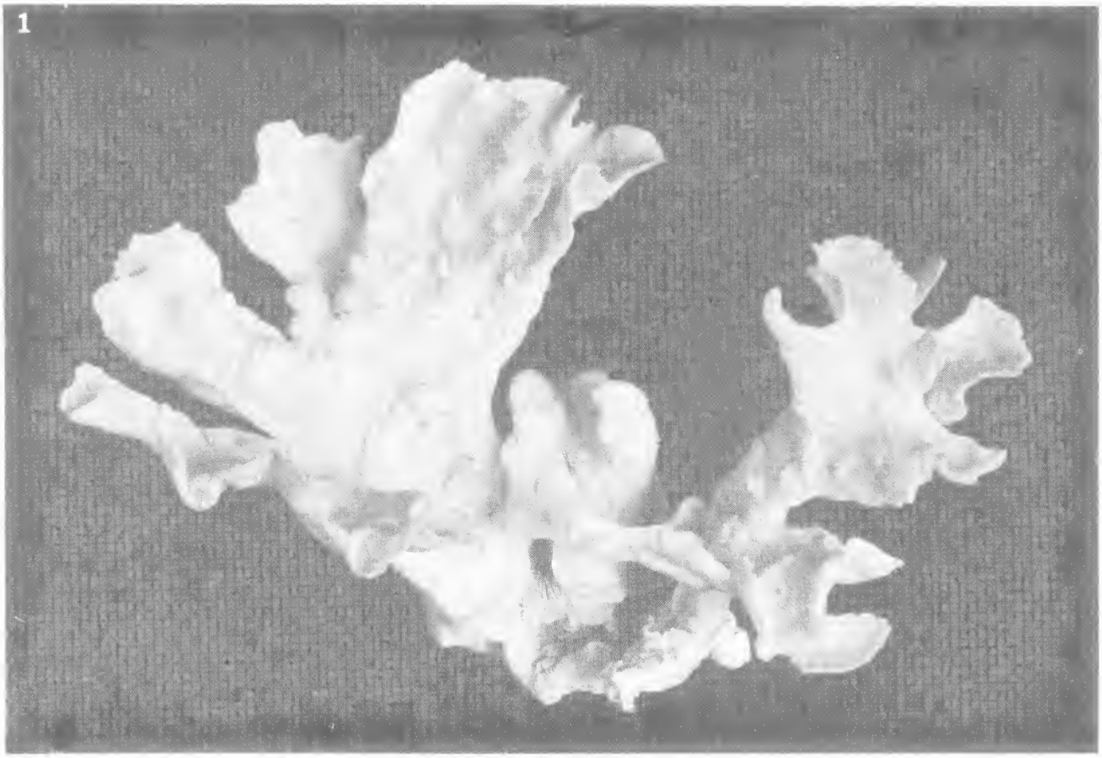
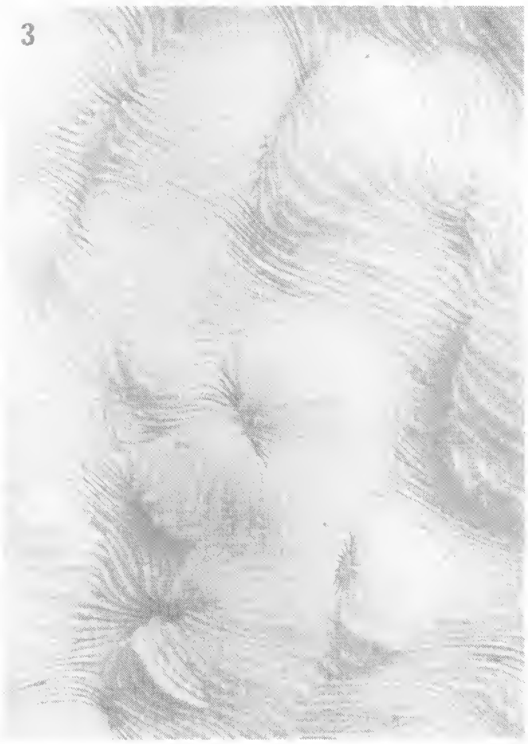
PLATE 16

FIGS. 1, 2: *Leptoseris glabra* n. sp. × 0·6; × 1·7. Orpheus I., Pioneer B., Palm Is. Group, GBR, 14 m, ZD 9496 (paratype).

FIG. 3: *L. glabra*. × 3. Channel to N. of Carter Reef, GBR, 5 m, BM 1979.4.7.5 (paratype).





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